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Systematics of targeted flat sedges (Cyperus, Cyperaceae) of the Americas, including a floristic analysis of an imperiled sedge-rich prairie community

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SYSTEMATICS OF TARGETED FLAT SEDGES (*CYPERUS*, CYPERACEAE) OF THE AMERICAS, INCLUDING A FLORISTIC ANALYSIS OF AN IMPERILED SEDGE-RICH PRAIRIE COMMUNITY

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ABSTRACT

The sedge family, Cyperaceae, is a large group with approximately 5,000 species distributed among ca. 100 genera. Sedges are economically and ethnobotanically important. They are conspicuous members of many floras around the world and provide vital food and cover for wildlife. The focus of this dissertation is on the genus *Cyperus*, which includes about 900 species. Due to its large size, advancements in knowledge of *Cyperus* are made in small "bites."

The molecular phylogenetics component of this research focused on New World *Cyperus*. Chapter 2 presents a phylogentic analysis employing sequences from the nuclear ITS region. Chapter 3 presents a more robust analysis using five genic loci, including sequences from nuclear ITS plus four plastid loci. This research was the first to estimate the phylogenetic position of the monotypic genus *Karinia*. *Karina* has been included in *Cyperus* in the past, and is here resolved as a member of the *Ficinia* clade which is consistently estimated as sister to the *Cyperus* clade in molecular studies. *Karinia* was embedded in a clade with *Sciproides*. Its morphology, including perennial habit, dense head-like inflorscences, and spirally-arranged floral scales, are consistent with that of *Scirpoides*. Another important result of this work is the resolution of the predominantly Central American *Cyperus andinus* and *C. seslerioides* as belonging to section *Leucocephali*. This study strongly supports section *Leucocephali*, whose members utilize C_3 photosynthesis, as sister to C_4 *Cyperus*. Members of section *Leucocephali* are adapted to open seasonally dry grasslands, which may be the ecological intermediary to the evolution of C_4 photosynthesis. Sampling for molecular studies included in this research enabled assessment of two taxonomic sections: *Luzuloidei* and *Diclidium*. The New World section *Luzuloidei*, which is composed of C_3 members, is strongly supported as monophyletic. A morphological synapomorphy in section *Luzuloidei* is the presence of two-keeled floral scales. Section *Diclidium*, which is diagnosed as having spikelets which break into one- to two-fruited segments upon maturity, is polyphyletic. Therefore, this unique mode of spikelet shattering arose independently at least twice. Results provided some insight into several taxonomic problems in the Umbellati group and in section *Strigosi*; however, a greater number of samples are needed to assess these problems.

The suspected relationship of the North American prairie species *Cyperus cephalanthus* to the South American *Cyperus rigens* species group was confirmed by the molecular phylogenetic analyses, as was the monophyly of the *C. rigens* group. *Cyperus cephalanthus* strongly resembles the South American *C. impolitus*. It was hypothesized that these taxa were morpholically indistinguishable. Morphometric analysis showed that several characters are statistically different, includeing floral scale dimensions, achene width, and achene shape. However, results of Principal Components Analisis (PCA) suggest that *Cyperus cephalanthus* and *C. impolitus* are the same morphological species. Results of PCA of *Cyperus rigens* and several of its infraspecific taxa were inconclusive, highlighting the need for more work with this highly variable South American taxon.

Coastal prairie is one of the most imperiled habitats in North America. It is in this habitat where *Cyperus cephalanthus* is found, with fewer than 20 known populations in North America (Louisiana and Texas). This research included a floristic survey of wet coastal prairie sites in southwestern Louisiana. This work was partly stimulated by the preference of *Cyperus cephalanthus* for this habitat, and further

motivated by the discovery of several promising prairie remnants quadrupaling the aerial extent of known coastal prairie in Louisiana. The wet coastal prairie flora included 512 minimum-rank taxa, with 461 being native. A total of 255 were estimated to be ecological conservative and characteristic of coastal prairie, with the balance consisting of weedy elements taking advantage of disturbance and habitat alteration. The wet coastal prairie was rich in sedges, with 72 species among nine genera. *Cyperus* was the most species rich genus in the entire wet prairire flora with 20 species. Coefficients of conservatism (C-values) were assigned to each taxon in the wet prairie flora. These C-values will allow computation of various Floristic Quality Indices (FQI) for sites ranging from unplowed prairie remnants to *de novo* restorations.

CHAPTER 1.
GENERAL INTRODUCTION

This section will serve to connect the chapters to follow and to generally orient the reader. The reader will be spared an exhaustive literature review here since pertinent literature is reviewed in the chapters below. The focal taxon and consistent element of this research is the genus *Cyperus* (Cyperaceae), which is a widely distributed group containing ca. 900 species. *Cyperus* is most diverse in the tropics and subtropics, and extends into temperate regions (Goetghebeur 1998). The lectotype for *Cyperus* is *C. esculentus* (Britton 1907).

Chapter 2 presents a phylogenetic analysis of *Cyperus* employing sequences from the nuclear ITS region; this chapter has been published (Reid et al. 2014). Chapter 3 presents a more robust phylogenetic analysis of *Cyperus* based on sequences from five genic loci. The analysis presented in Chapter 3 includes an expanded sampling of taxa based on field work in southern Florida, Uruguay, and samples provided to the author by a colleague in Mexico. A manuscript derived from Chapter 3 has been accepted for publication in the journal *Plant Ecology and Evolution*. As this dissertation is being completed, so too is the revised manuscript for publication.

Chapter 4 presents a morphometric analysis of the primarily South American *Cyperus rigens* species group. This group includes one North American species, *Cyperus cephalanthus*, which is an apparent rare endemic growing in wet coastal tall-grass prairies on the northern Gulf of Mexico in Louisiana and Texas. This name has also been applied to similar plants in subtropical South America. South American relatives bearing the name *Cyperus impolitus* also grow in humid grasslands with a high level of floristic overlap with North American prairies, especially at the genus level. The most important objective of the morphometric study was to determine if *Cyperus cephalanthus* and *C. impolitus* were distinguisahable based on morpholocial evidence. A secondary objective of Chapter 4 was to gain better taxonomic clarity for *Cyperus rigens* and its infraspecfic taxa.

Chapter 5 presents a floristic analysis of the wet coatstal prairie habitat based on surveys of nine study sites in southwestern Louisiana. It is this grassland type that supports *Cyperus cephalanthus*, a focal taxon in all components of this work. This expression of coastal prairie has been negelected scientifically. The objectives were to generate a baseline list of plants, to gain information on vegetation associations present on this prairie type, and to assign coeffificients of conservatism which will be useful for future site-level Floristic Quality Assessments.

There are many scientific names used in the text of this dissertation. To preserve continuity, authors of scientific names not listed in Appendices 3, 4 and 6 are given in the text at first use. Scientific names that are included in these appendices are not accompanied by the names of their authors in the text. Authors for generic names are given in the text at first use.

CHAPTER 2.
PHYLOGENTIC INSIGHTS INTO NEW WORLD *CYPERUS* (CYPERACEAE) USING NUCLEAR ITS SEQUENCES*

Introduction

Even when treated in its most narrow taxonomic concept, *Cyperus* L. is the second largest sedge genus. Typical *Cyperus* (sensu stricto) is recognized as having an herbaceous habit with basally disposed leaves, a terminal anthelate inflorescence immediately subtended by leafy bracts, spikes clustered on often elongate peduncles (rays), laterally flattened spikelets with two-ranked floral scales, and flowers lacking a perianth. Most of these characteristics can be seen in Figure 1 A-D. *Cyperus* includes several well-known and interesting members. *Cyperus papyrus* was an important source of paper in the early history of western civilization (Bryson & Carter 2008). The cosmopolitan *Cyperus esculentus* (chufa or yellow nutsedge) possesses edible tubers. This species is also valued as an important wildlife food, while regarded in some settings as a weed (Bryson & Carter 2008). *Cyperus rotundus* (purple nutsedge) has been branded the world's worst agricultural weed (Holm et al. 1977). Many *Cyperus* species (and other sedges) are ecologically important and are valuable to wildlife.

The question "What is *Cyperus*?" has not always been easy to answer, as evidenced by the considerable variation in the circumscription of the group (Kükenthal 1935-1936, Koyama 1961, Haines & Lye 1983, Goetghebeur 1998). *Cyperus* sensu stricto, as in Goetghebeur's (1998) scheme, is paraphyletic (Muasya et al. 1998, Simpson et al. 2007, Muasya et al. 2009a, b, Larridon et al. 2011c, 2013). With *Cyperus* as its core genus, the well-supported *Cyperus* clade also includes the genera *Alinula* Raynal, *Androtrichum* (Brongn.) Brongn., *Ascolepis* Nees ex Steudel, *Courtoisina* Soják, *Kyllinga* Rottb., *Kyllingiella* R. Haines & Lye, *Lipocarpha* R. Br., *Oxycaryum* Nees *Pycreus* P. Beauv., *Queenslandiella* Domin, *Remirea* Aublet, *Sphaerocyperus* Lye, and *Volkiella* Merxm. & Czech (Muasya et al. 2009a). Some of these genera have been treated as infra-generic taxa of *Cyperus* in more inclusive classifications (e.g. Haines & Lye 1983). Based on research to date, the only consistent division in the *Cyperus* clade is based on the C_3/C_4 photosynthetic pathways (Muasya et al. 2001, Muasya et al. 2002, Besnard et al. 2009, Larridon et al. 2011c, 2013). In their study of C_3 *Cyperus*, Larridon et al. (2011c) recovered a C_3 grade basal to a strongly supported C_4 clade. The division of *Cyperus* into two groups based on presence of Kranz anatomy, an anatomical characteristic of the C_4 pathway, was originally suggested by Rikli (1895). This division was advocated by Goetghebeur (1989), who proposed that *Cyperus* sensu stricto be split into two subgenera: *Anosporum* (Nees) C.B. Clarke, containing species lacking Kranz anatomy and possessing C_3 photosynthesis; and *Cyperus*, comprising species with Kranz anatomy and C_4 photosynthesis. This classification is also proposed by Larridon et al. (2011c, 2013).

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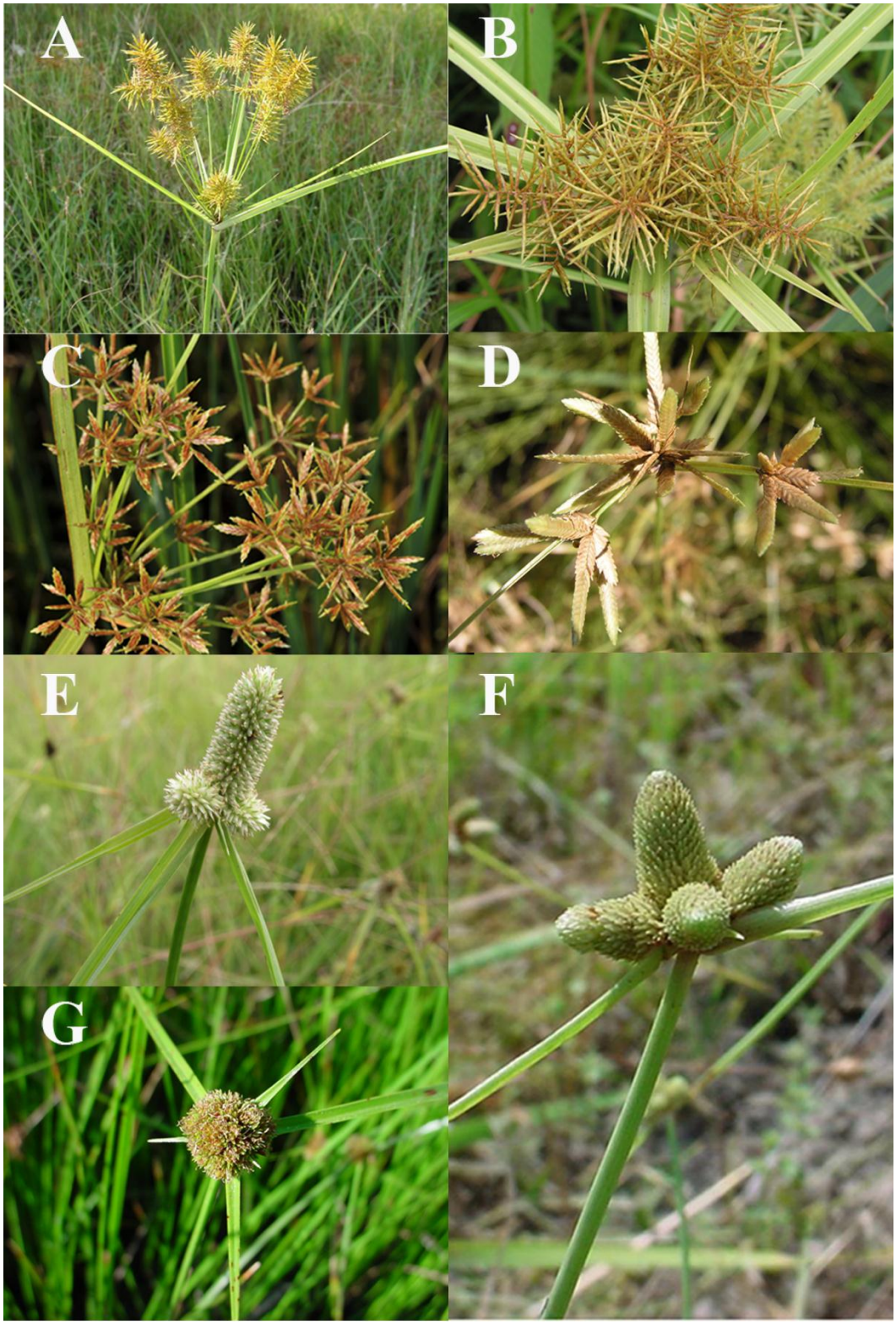

Figure 1. Representative members of the *Cyperus* clade. **A.** *Cyperus strigosus*. **B.** *Cyperus odoratus*. **C.** *Cyperus haspan*. **D.** *Pycreus lanceolatus*. **E.** *Kyllinga odorata*. **F.** *Lipocarpha maculata*. **G.** *Oxycaryum cubense.* Images. A, B, D-F by R. Carter, C by T. Jones.

Recent research supports a broader circumscription of *Cyperus*, with the *Cyperus* clade containing ca. 950 species (Muasya et al. 2009b, Larridon et al. 2013). Relationships among selected members of the *Cyperus* clade possessing C_3 photosynthesis were estimated by Larridon et al. (2011c). A phylogenetic study of C_4 segregates *Kyllinga* and *Pycreus* has been completed (Larridon et al., 2013), while a study of *Lipocarpha* is underway (K. Bauters, pers. comm.). The studies cited above include mainly Old World members of the *Cyperus* clade. The purpose of this study is to present an exploratory phylogenetic analysis of 85 in-group *Cyperus* s.l. taxa that are primarily New World natives, using sequences from the nuclear internal transcribed spacer (ITS) region. Specific objectives were to perform a preliminary assessment of the sectional classification presented in Kükenthal's (1935-1936) monograph of *Cyperus*, to evaluate relationships among species and species complexes represented, and to determine directions for more comprehensive work in the future.

Materials and Methods

A total of 95 ingroup sequences representing 85 taxa and 14 outgroup taxa were included in this analysis (listed in Table 1). Materials for most ingroup taxa were collected by the author from the southeastern United States (Louisiana, Florida, Georgia, and Texas) in 2010 and 2011, and during an expedition to northeastern Argentina in February of 2011. Materials of several taxa were provided by other botanists. Sequences of some ingroup and most outgroup taxa were obtained from GenBank (http://www.ncbi.nlm.nih.gov/genbank/). While a broader circumscription of *Cyperus* is warranted by previous work (reviewed above), generic limits in this paper follow the more exclusive system of Goetghebeur (1998), to provide maximum contrast in evaluating phylogentic hypothesis presented herein. Genera included in the ingroup are *Cyperus*, *Kyllinga*, *Lipocarpha*, *Oxycaryum*, *Pycreus*, and *Queenslandiella* (Table 1). Images of representatives of these genera, with the exception of *Queenslandiella*, are presented in Figure 1. Outgroup taxa include Cyperaceous genera basal to tribe Cypereae, as well as *Juncus* L. and *Oxychloe* Phil. (Juncaceae).

Materials collected by the author were placed in silica gel upon collection for drying. Voucher specimen information and GenBank accession numbers are provided in Table 1. DNA extractions were carried out using the DNeasy Plant Minikit (Qiagen, Germantown, MD, USA). The ITS region (ITS 1 + 5.8S rDNA+ ITS 2) was amplified by polymerase chain reaction (PCR) using forward primer sef 17 (5'-ACGAATTCATGGTCCGGTGAAGTGT TCG-3') and reverse primer ser 26 (5'-TAGAATTCCCCGGTTCGCTCGCCGTTAC-3') (Sun et al., 1994). This region was amplified with a touchdown protocol using the parameters 95°C, 3 min; 9X (95°C, 1 min; 55°C, 1 min, reducing 0.5°C per cycle; 72°C, 1 min + 4 sec per cycle); 19X (95°C, 1 min; 55°C, 1 min; 72°C, 1 min); 72°C, 7 min; 4°C until stopped. Each PCR reaction consisted of 0.5 µL MasterAmp™ *tfl* polymerase (Epicentre Technologies, Madison, WI), 12.5 µL buffer GN, 8 µL sterile water, 1 µL of each primer, and 2 µL template (diluted to 10^{-1}), totaling 25 µL. The ITS region of *Isolepis carinata* was amplified using the same PCR cycle protocol but with the reaction consisting of 0.25 µL Phusion® polymerase (New England Biolabs®, Inc., Ipswich, MA), 5 µL buffer HF, 0.5 µL $MgCl_2$, 14.25 µL sterile water, 1 µL of each primer, and 2 µL template. Amplification of the ITS region with Phusion polymerase failed for the vast majority of taxa with which it was attempted, but for some reason was very successful with *Isolpeis carinata*, while the *tfl* polymerase reaction was not successful with *I. carinata*. Gel electrophoresis was performed to confirm success of PCR reactions. PCR products were shipped on dry ice to Beckman Coulter Genomics, Danvers, MA, for sequencing using the amplification primers. Returned sequences were subjected to a BLAST search (Altschul et al. 1990) to verify that the sequences belonged to the

target organism and not a contaminant. Sequences were edited using Sequencher v. 4.2.2 (Gene Codes Corporation). Sequences were aligned with MAFFT v. 7.017 (Katoh et al. 2002) using the MAFFT plug-in of Geneious v. 6.1.5 (Drummond et al. 2010) using default settings. The multiple sequence alignment of nrITS sequences was partitioned into ITS1, 5.8S, and ITS2 and analyzed under maximum likelihood and Bayesian frameworks. The maximum likelihood search was performed in RAxML v. 7.2.6 (Stamatakis 2006) using the generalized time-reversible (GTR) model of sequence evolution with node support assessed with 500 bootstrapped pseudoreplicate datasets. For the Bayesian analysis, the appropriate model of sequence evolution was selected for each data partition using jModelTest v. 2.1.3 (Guindon & Gascuel 2003, Darriba et al. 2012). Models selected using the Akaike Information Criterion (AIC) were GTR + Γ + I for ITS1 and ITS2, and HKY + Γ + I for the 5.8S region. Bayesian analysis was conducted using MrBayes v. 3.1.2 (Ronquist & Huelsenbeck 2003) via the CIPRES Science Gateway (Miller et al. 2010). The Bayesian analysis consisted of 4 parallel runs using one heated (temp=0.5) and three cold chains per run for 30,000,000 generations sampling every 1,000 generations. All parameters of sequence evolution models were unlinked across partitions. Convergence of each run was assessed by ensuring that potential scale reduction factors (PSRF) reported in MrBayes were close to 1 and effective sample size (ESS) values were greater than 200 in Tracer v. 1.5 (Rambaut & Drummond 2007). A Bayesian majority-rule consensus tree was produced from the stationary distribution after discarding the first 25% of the sampled trees as burn-in. A tree summarizing both analyses was produced by mapping posterior probabilities and bootstrap proportions onto the Bayesian consensus tree using SumLabels v. 1.0.0, part of the DendroPy Phylogenetic Computing Library v. 3.12.0 (Sukumaran & Holder 2010). The tree was inspected and edited using Fig Tree v. 1.3.1 (Rambaut 2006-2009) and prepared for publication using Adobe® Illustrator® CS4.

Results

Sequence length ranged from 539 bp to 624 bp. Including gaps, the aligned matrix had 685 characters. Sequencing required minimal use of ambiguous character states. Of the 74,665 cells in the matrix, 39 (~0.5%) were occupied by ambiguous character states. The phylogenetic tree resulting from this analysis is presented in Figures 2 and 3. Ingroup taxa compose a well-supported clade (bootstrap proportion (bsp)/posterior probability (pp) = 75/1.00). Ingroup taxa possessing C_3 photosynthesis form a grade (Fig. 2) that is basal to a strongly-supported (bsp/pp = 94/1.00) C_4 clade (Fig. 3). Resolution is better and branch lengths are longer in the C_3 basal grade (Fig 2). Resolution at deep to intermediate levels within the C_4 clade is poor as evidenced by several polytomies (Fig. 3). The pantropical *Cyperus cuspidatus* is sister to the remainder of the C_4 clade (Fig. 3), the same phylogenetic position as reported in other studies (Muasya et al. 2002, Larridon et al. 2011c, 2013).

Kyllinga, *Lipocarpha*, *Oxycaryum*, *Pycreus*, and *Queenslandiela* are embedded within *Cyperus* (Figs. 2, 3). *Kyllinga* is monophyletic with strong support (Fig. 3; bsp/pp = 99/1.00). *Lipocarpha* is paraphyletic (Fig. 3) and in the study of Larridon et al. (2013), where it fell within a clade also containing *Ascolepis* and *Volkiella* (not sampled here). *Lipocarpha* (Fig. 1F) has generally not been included within *Cyperus*, but consistently falls within it in molecular studies (Muasya et al. 1998, Muasya et al. 2001, Muasya et al. 2002, Simpson et al. 2007, Muasya et al. 2009a, b, Larridon et al. 2013). Prior to the availability of molecular evidence, Koyama (1961) was apparently the only author to have treated *Lipocarpha*, which has highly reduced spikelets, within *Cyperus*. *Oxycaryum cubense* is sister to a clade containing *Cyperus dichrostachyus*, *C. difformis*, and *C. fuscus* which are members of section *Fusci* (Kunth) C.B. Clarke

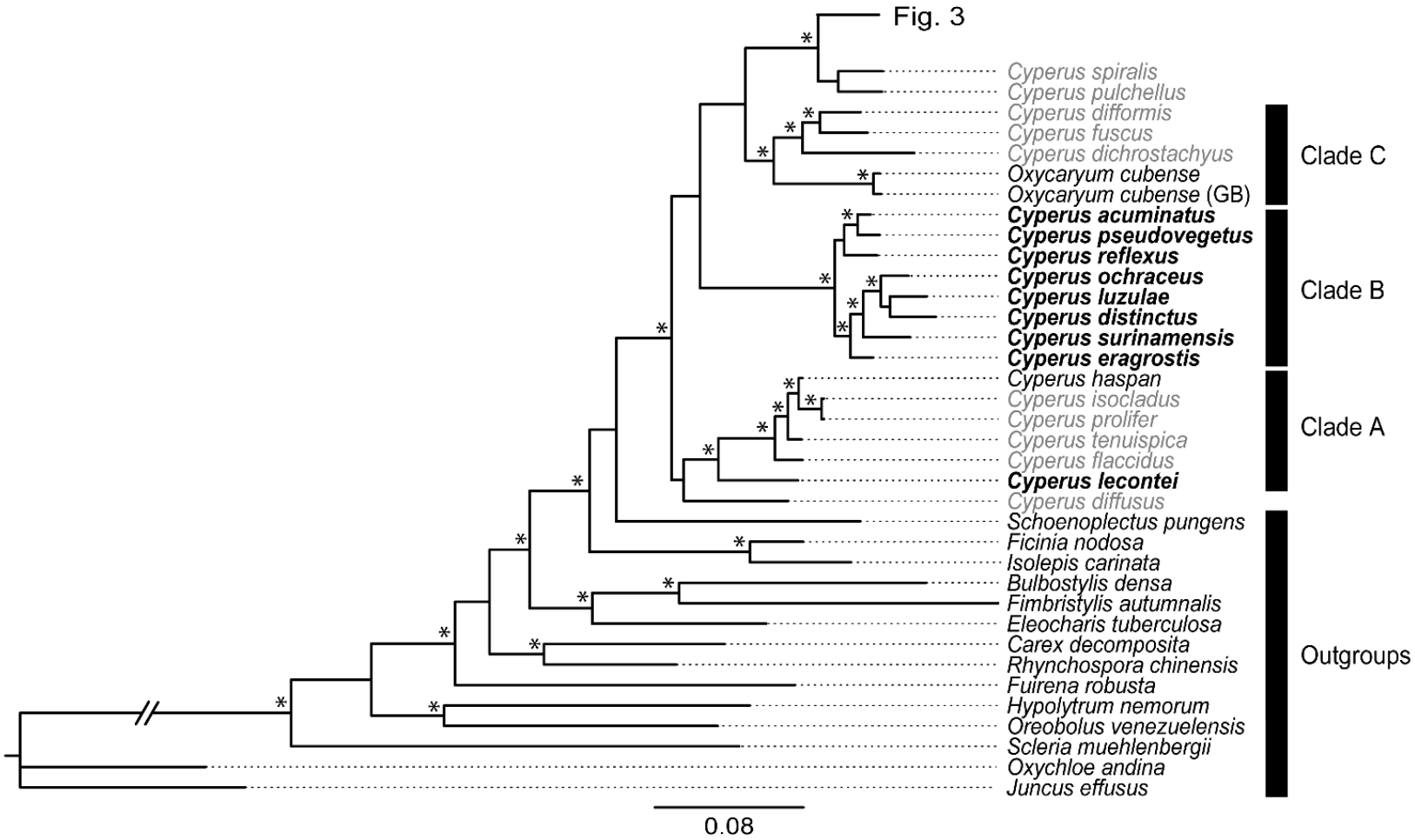

Figure 2. Outgroups and C_3 grade. Bayesian majority-rule consensus tree based on maximum likelihood and Bayesian analyses of nuclear ITS sequences of *Cyperus*. Nodes with bootstrap proportions ≥ 75 or posterior probabilities ≥ 0.85 are labeled with an asterisk (*). Taxon name font color/style is according to native geographic distribution. Old World taxa are in gray font, pantropical taxa are in regular black font, and New World taxa are in bold black font. Native ranges of taxa were determined by consulting Schippers et al. (1995), Tucker (2002), Tucker et al. (2002), Lunkai et al. (2010), and eMonocot Team (2013). Lettered clades are discussed and exact support values are reported in text.

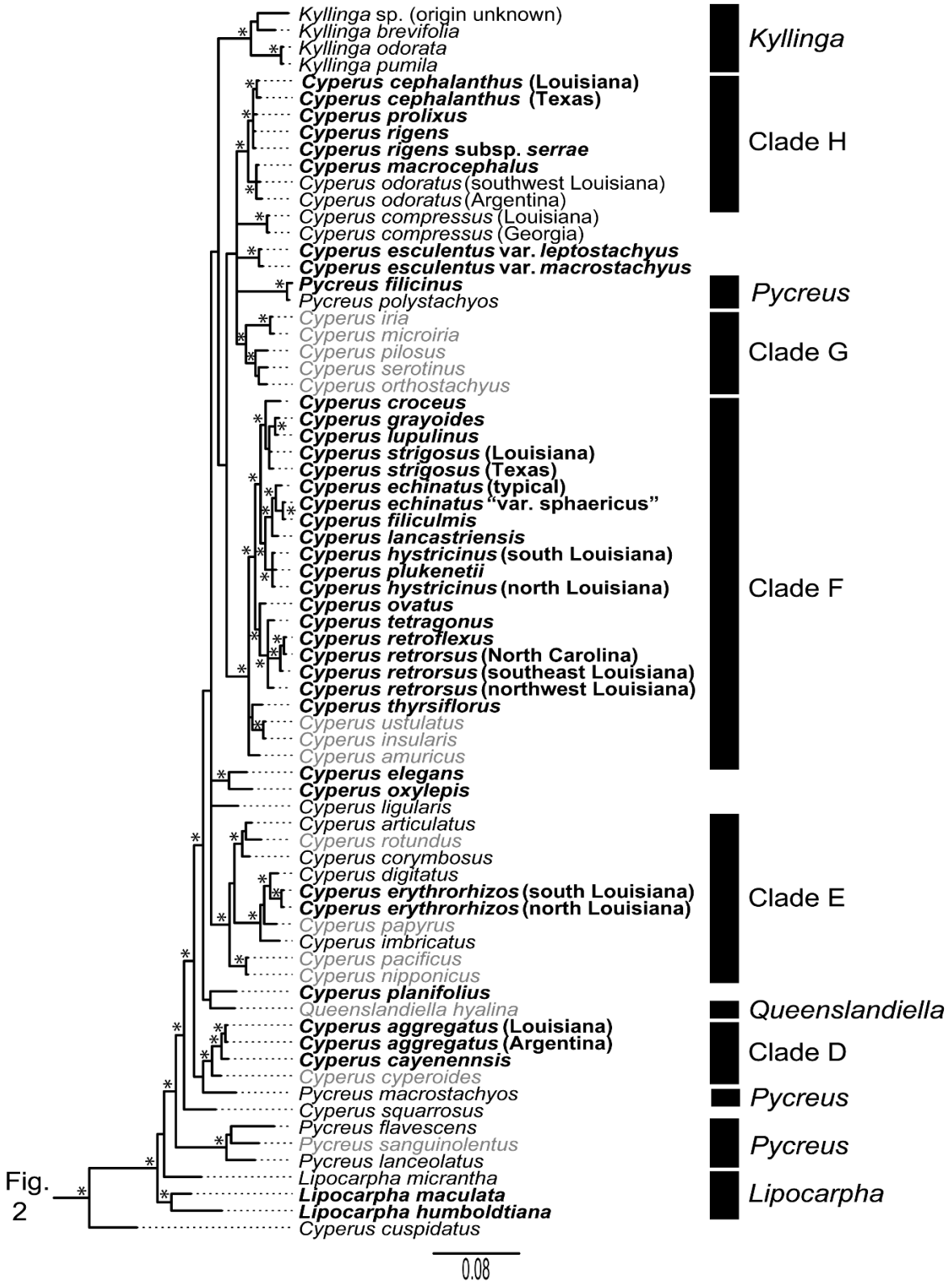

Figure 3. C_4 clade. Bayesian majority-rule consensus tree based on maximum likelihood and Bayesian analyses of nuclear ITS sequences of *Cyperus* (continued).

(Kükenthal 1935-1936) (Clade C, Figure 2). Clade C is well-supported (bsp/pp = 94/1.00). *Pycreus* is polyphyletic, with representatives associated with three widely separated clades (Fig. 3). *Pycreus* was also polyphyletic in the analysis of Larridon et al. (2013). *Queenslandiella* is monotypic, represented by *Q. hyalina* (*Cyperus hyalinus* Vahl). The phylogenetic position of *Q. hyalina* is poorly resolved (Fig. 3).

Within the C_3 grade (Figure 2), Clade A (bsp/pp = 93/1.00) consists almost entirely of members of section *Haspani* (Kunth) C.B. Clarke, with the lone exception being *C. flaccidus* of section *Graciles* Benth. (Kük.). *Cyperus isocladus* is treated as a synonym of *C. prolifer* by Govaerts and Simpson (2007), a treatment supported by results of this analysis (Clade A, Fig 2). Clade B (bsp/pp = 100/1.00) consists of members of section *Luzuloidei* (Kunth) C. B. Clarke. This clade will be discussed more fully below.

Within the C_4 clade (Figure 3), clades D - H have strong support. For Clade D, bsp/pp = 86/0.99. Several taxonomic sections are represented in Clade E (bsp/pp = 83/1.00), which includes species with pantropical distributions such as *Cyperus articulatus*, *C. corymbosus*, and *C. digitatus*, several strictly Old World taxa such as *C. nipponicus*, *C. pacificus*, *C. papyrus*, and *C. rotundus*, and the New Word *Cyperus erythrorhizos.* The majority of taxa in Clade F (bsp/pp = 95/1.00) are native to North America, with the exception of *Cyperus insularis* and *C. ustulatus* which are both endemic to New Zealand, and the east Asian *C. amuricus* Maxim. Members of Clade G (bsp/pp = 67/0.93) are all Old World natives. Clade H (bsp/pp = 82/0.99) comprises two sub-clades. The sub-clade containing *Cyperus macrocephalus* and *C. odoratus* corresponds to subgenus *Diclidium* (Schrader ex Nees) C. B. Clarke. Support for the *Cyperus odoratus*-*C. macrocephalus* clade is strong (bsp/pp = 83/1.00). The other sub-clade within Clade H has moderately strong support (bsp/pp = 81/0.81) and shows a close relationship between *Cyperus cephalanthus* and *C. rigens*, members of the *C. rigens* complex that also includes *C. impolitus*, and several other primarily South American taxa (Pedersen 1972).

Discussion

Results support an expanded concept of *Cyperus* and resolve a C_3/C_4 split, adding support to the work of other researchers (Muasya et al. 1998, 2002, 2009a, b, Simpson et al. 2007; Larridon et al. 2011c, 2013). Short branch lengths and poor resolution, especially at intermediate depths, are evident in the C_4 clade in this phylogentic hypothesis. Resolution is improved closer to tips of the tree (Fig. 3). Similar results were reported by other workers (Larridon et al. 2013). Limited taxon sampling does not allow rigorous evaluation of sectional taxonomy and biogeography, but does represent an important step toward that end. There are apparent relationships among several ingroup taxa at smaller scales that are worthy of discussion.

In the C_3 grade, section *Luzuloidei* is monophyletic (Clade B, Fig. 2). This group was also reported by Larridon et al. (2011c) to be monophyletic in their Bayesian and maximum likelihood analyses of the chloroplast markers *rpl32-trnL* and *trnH-psbA* and nuclear ETS1. A synapomorphy uniting the members of section *Luzuloidei* represented in this study is the presence of basally two-keeled floral scales (Denton 1978). Denton's (1978) view that her circumscription of the *Luzulae* group, consisting of the New World representatives of section *Luzuloidei* sensu Kükenthal, is natural is supported by the results of this study and results of Larridon et al. (2011c). The ITS phylogeny, which includes eight of the 10 species treated by Denton (1978) in a phenetic study involving clustering and discriminant analysis, supports her conclusion that *C. ochraceus* and *C. distinctus* are closely related. However, results of this study did not

confirm close relationships between *C. luzulae* and *C. pseudovegetus* and between *C. acuminatus* and *C. eragrostis* Lam., which were supported by Denton's (1978) phenetic data.

Cyperus subgenus *Diclidium* (formerly *Torulinium* (Desv.) Kük.) is represented in this analysis by *C. macrocephalus* and two samples of *C. odoratus*. These species are considered conspecific by Tucker (1984). Tucker et al. (2002) report eight species in this group. Members of subgenus *Diclidium* are diagnosed by having rachillas that disarticulate at the base of each floral scale, the spikelets thus splitting into one-fruited segments (Tucker et al. 2002). In the ITS analysis, subgenus *Diclidium* is monophyletic, highly derived, and apparently has some very close relatives not possessing the spikelet-shattering mode of *Diclidium*. Provided that greater taxon sampling continues to support the monophyly of *Diclidium*, a reduction in rank from subgenus to section may be appropriate.

The ITS tree provides preliminary evidence that the C_4 section *Thunbergiani* (C. B. Clarke) Kük. is artificial, because its representatives in the study, *Cyperus cephalanthus*, *C. insularis*, *C. planifolius*, *C. rigens*, and *C. ustulatus*, do not form a clade. Section *Thunbergiani* is diagnosed by a robust, usually tall, habit, biennial or perennial lifespan, long leaves and bracts, numerous spikelets per spike, and floral scales that are often reddish (Clarke 1897). Morphologically, the group seems well-defined, but results of this study suggest it is artificial. Suspicious about the position of *Cyperus planifolius*, DNA extraction and amplification was repeated from silica dried material and directly from the voucher specimen, and identical sequences were recovered.

In addition to members of section *Thunbergiani*, the strongly supported Clade F (Figure 3) comprises members of several other mariscoid sections, fide Kükenthal (1935-1936), including *Laxiglumi* (C. B. Clarke) Kük., *Strigosi* Kük., *Tetragoni* Kük., and *Umbellati* (C. B. Clarke) Kük., suggesting their artificial nature as suspected by Carter and Jones (1997) based upon morphological incongruities. Members of Clade F are mostly New World species centered in North America with two taxa, *Cyperus thyrsiflorus* and *C. croceus*, also extending into South America (Tucker et al. 2002). The presence of New Zealand endemics *Cyperus ustulatus* and *C. insularis* and the Asian *C. amuricus* is of interest. If these taxa are truly closely related to the American taxa in Clade F, long distance dispersal could explain this situation, as sedges, with their small fruits, can be dispersed by animals as well as on ocean currents (Kern 1974).

Cyperus plukenetii and *C. hystricinus* are remarkable among sedges of the southeastern United States in their adaptation to excessively well-drained sandy soils, and Clade F (Fig. 3) suggests a close relationship between these taxa previously supported only by morphological and ecological evidence (Carter 1984). Other species in Clade F that are adapted to dry, sandy soils include *C. grayoides*, *C. lupulinus*, and *C. filiculmis*, all members of section *Laxiglumi*.

Clade F (Fig. 3) shows a close, but not sister, relationship between *Cyperus echinatus* "var. *sphaericus*" [=*C. ovularis* (Michx.) Torr. var. *sphaericus* Boeck.] and the typical expression of *C. echinatus*. *Cyperus echinatus* "var. *sphaericus*" is sister to *C. filiculmis* in this analysis, and their ITS sequences are actually identical. In the southeastern United States, *Cyperus echinatus* "var. *sphaericus*" and *C. filiculmis* are characteristic species of sandy soils in fire-driven *Pinus palustris* Mill. woodlands. The latter usually inhabits slightly drier, sandier sites than the former. Conversely, typical *C. echinatus* is more of a weedy plant generally associated with mesic, finer-textured soils. In this study, *C. echinatus* "var. *sphaericus*" and *C. filiculmis* were collected from different sites on different dates, and PCR amplification was

conducted in different batches on different dates, so cross-contamination does not seem a likely explanation of these taxa having identical ITS sequences. Additional sequencing of the ITS region in all three taxa in this clade will be carried out to determine consistency of sequences. It is possible that *C. echinatus* "var. *sphaericus*" is a result of hybridization between typical *C. echinatus* and *C. filiculmis*. If the hybridization hypothesis is correct, PCR could have amplified an ITS copy of *C. filiculmis* in material of "var. *sphaericus*". The use of bacterial cloning when working with ITS, as done by Siripun and Schilling (2006) in *Eupatorium* L. (Asteraceae), plus sequencing markers from other genomes, would be helpful in elucidating the true identity and proper taxonomic placement of "var. *sphaericus*".

Cyperus ovatus Baldwin has an essentially Floridian distribution, extending westward along the Gulf coast into Louisiana and northward along the Atlantic coast to North Carolina. It was segregated by Small (1933), albeit under different names (*Cyperus pollardii* Britton, *C. winkleri* Britton & Small). Subsequently it was maintained as a species by Carter (1984) and Tucker et al. (2002). Presumably because of superficial similarity in gross features of inflorescence form, some workers (e.g. Godfrey & Wooten 1979, Wunderlin & Hansen 2003) have treated *C. ovatus* as a synonym of *C. retrorsus* Chapm. despite a number of differences between the two taxa, including floral scale posture (ascending vs. appressed) and color (yellow-stramineous vs. reddish brown), achene shape (elliptic vs. oblong), and inflorescence bract posture (divaricate vs. ascending). The position of *C. ovatus* vis-à-vis *C. retrorsus* in Clade F supports its treatment as a distinct taxon at the rank of species.

Conclusions

The poor resolution of deeper nodes in the C_4 *Cyperus* clade has been referred to as a hard polytomy (Reynders et al. 2010; Larridon et al. 2013). Larridon et al. (2013) regard C_4 photosynthesis as a key innovation which allowed invasion of hot, dry, high-irradiance sites, and sites experiencing fire or chemical stress, leading to rapid diversification. Perhaps the C_4 clade can be better resolved using large data sets generated by next generation sequencing technology, such as 454 sequencing.

It would be informative to sample putative relatives of members of Clade F which have more westerly distributions such as *Cyperus hermaphroditus* (Jacq.) Standley, *C. pseudothyrsiflorus* (Kük.) J.R. Carter & S.D. Jones, *C. lentiginosus* Millsp. & Chase, *C. floribundus* (Kük.) J.R. Carter & S.D. Jones, *C. manimae* Kunth, *C. hypopitys* G.C. Tucker, to see if Clade F continues to expand. Many members of Clade F grow in drier habitats. It would also be prudent to sample additional species of dry sandy soils such as *Cyperus schweinitzii* Torr., *C. houghtonii* Torr., and *C. grayi* Torr., which are members of section *Laxiglumi*. This section is represented by several taxa in Clade F. In all future research, additional markers from nuclear and plastid regions should be employed to increase the confidence of phylogenetic hypotheses.

CHAPTER 3.
MOLECULAR SYSTEMATICS OF SELECTED LINEAGES OF CYPERUS (CYPERACEAE) BASED ON ANALYSES OF DNA SEQUENCES FROM FIVE GENIC LOCI

Introduction

Cyperus L. is a large, ecologically diverse, and economically important sedge group (Simpson & Inglis 2001, Bryson & Carter 2008). For many years, the circumscription of *Cyperus* was problematic. Early molecular studies resolved a well-supported clade composed of *Cyperus sensu stricto* plus up to thirteen other embedded genera (Simpson et al. 2007, Muasya at al. 2009a, b). The paraphyly of *Cyperus* has recently been addressed by formal inclusion within *Cyperus* of segregate genera embedded in the *Cyperus* clade (Larridon et al. 2011c, Larridon et al. 2014; Bauters et al. 2014).

Phylogenetic hypotheses of *Cyperus* consistently resolve a grade composed of taxa possessing C_3 photosynthesis that is basal to a strongly supported C_4 clade (Muasya et al. 2001, 2002, Larridon et al. 2011c, 2013, Reid et al. 2014). Having apparently evolved once, the C_4 photosynthetic pathway is a synapomorphy in *Cyperus*. The evolution of C_4 photosynthesis may have spurred rapid diversification in *Cyperus* by allowing colonization of drier, sunny, and fire-driven habitats (Larridon et al. 2013). Most taxa included in this study utilize C_4 photosynthesis, and many, particularly those endemic to eastern North America, occur in dry, open habitats subject to recurring fire.

Many of the ca. 950 *Cyperus* species have not been included in phylogenetic studies. Due to the massive size of the genus, a "complete" phylogenetic hypothesis for *Cyperus* is not imminent. This study was motivated by several taxonomic and biogeographic questions and has the following objectives: 1) to estimate the phylogenetic position and tribal placement of *Karinia* Reznicek & McVaugh, which has previously been included in *Cyperus*; 2) to estimate relationships of *Cyperus* sections *Leucocephali* Chermezon ex Kük. and "*Dichostylis* (P. Beauv.) Baillon" to C_4 *Cyperus*; 3) to test the monophyly of *Cyperus* section *Diclidium* (Schrad. ex Nees) Griseb.; 4) to assess taxonomic problems in *Cyperus* section *Strigosi* Kük. and in the Umbellati group; and 5) to elucidate relationships within the *Cyperus rigens* species group. This study includes samples of many taxa outside of primary groups of interest, adding an exploratory aspect to this work with the intentions of gaining additional phylogenetic and biogeographic insights and identifying future research problems.

Scirpus, Cyperus, or *Karinia?*

Karinia is a monotypic genus that is endemic to Mexico. Its only species, *Karinia mexicana*, was previously included in *Scirpus* L. as *Scirpus orbicephala* Beetle on the basis of having spirally arranged floral scales, a character state typical of tribe Scirpeae. Koyama and McVaugh (1963) transferred this species to *Cyperus* because of its basally disposed leaves and presence of empty floral scales at the base of each spikelet (lowest floral scales in *Scirpus* are flower-bearing). Later, Reznicek and McVaugh (1993) determined that this Mexican endemic was sufficiently unique, having dense spherical spikes and spirally-arranged floral scales, to warrant erection of a new genus, *Karinia*, which they placed in tribe Cypereae due to its *Cyperus*-type embryo. The phylogenetic position of *Karinia* has not previously been estimated and its taxonomic classification has not been evaluated using molecular evidence.

Which C_3 taxa are most closely related to the C_4 clade?

As mentioned above, C_4 photosynthesis is a synapomorphy in *Cyperus*. Larridon et al. (2011c) resolved a clade containing *Cyperus schomburgkianus* plus three species of *Kyllingiella* as sister to C_4 *Cyperus*. Larridon et al. (2001a) lumped *Kyllingiella* with *Cyperus* on the basis of morphological and molecular evidence and assigned these species to section *Leucocephali*, to which *C. schomburgkianus* had previously been assigned. The pantropical section *Leucocephali* is diagnosed by consisting of small to medium sized plants with dense head-like inflorescences, having pale-colored floral scales, and growing in open grasslands subject to seasonal drying (Larridon et al. 2011c, Simpson 1990). The ecological adaptation to upland habitats of section *Leucocephali* may be transitional toward the evolution of C_4 photosynthesis, a photosynthetic pathway that enhances drought tolerance (Larridon et al. 2011c). Included in this study are *Cyperus seslerioides* and *C. andinus*, which are distinguished by Kükenthal (1935-1936) but considered conspecific by more recent authors (Tucker 1994, Gómez-Laurito 2003, Govaerts et. al 2016). *Cyperus seslerioides* (including *C. andinus*) is common in Mexico (Tucker 1994) and extends into South America to Argentina (Govaerts et al. 2016). *Cyperus seslerioides* and *C. andinus* were included in Kükenthal's (1935-1936) "section *Dichotsylis*"; this name is illegitimate (Huygh et al. 2010) and no name currently exists for this group. This group is likely artificial since it contains at least two species, *Cyperus meeboldii* Kük. and *C. michelianus* (L.) Link, confirmed to be C_4 plants (Bruhl & Wilson 2007, Larridon et al. 2011c). *Cyperus seslerioides* resembles members of section *Leucocephali* in having pale, head-like inflorescences, minutely papillose achenes (papillae lacking in the sample of *C. andinus* included in this study), and by growing in upland habitats (Simpson 1990, Tucker 1994). This research will provide examine the possible relationship between the included representatives of "section *Dichostylis*" and section *Leucocephali*, and relationships of both taxa to C_4 *Cyperus*.

Cyperus* section *Diclidium

Cyperus section *Diclidium* is characterized by a unique mode of spikelet shattering where the spikelet breaks into one-fruited segments (Kükenthal 1935-1936, Tucker 1994, Tucker et al. 2002). This research will test the null hypothesis that section *Diclidium* is monophyletic. *Cyperus odoratus* shares a corky spikelet rachilla with *Cyperus pedunculatus*, a species not previously classified in section *Diclidium*. This feature may have allowed water dispersal of fruits, accounting at least partly for the large, transoceanic ranges of these two species. Further investigation of a possible close relationship between these two taxa was suggested by Larridon et al. (2013). Due to their morphological dissimilarity, the null hypothesis is that the corky rachilla is a homoplastic trait.

Distinctness of *Cyperus stenolepis*

There has been inconsistency in the taxonomic treatment of *Cyperus stenolepis*, a wetland species endemic to the southeastern United States. Some authors (Tucker et al. 2002, Govaerts et al. 2016) do not recognize *Cyperus stenolepis*, treating it as a synonym of *C. strigosis*. Kükenthal (1935-1936) treated *Cyperus stenolepis* as *C. strigosus* var. *stenolepis* (Torr.) Kük. This treatment was retained (with reservations) by Horvat (1941). Morphologically, *Cyperus stenolepis* is more robust than *C. strigosus* and has longer and more remote floral scales. *Cyperus stenolepis* differs ecologically from *C. strigosis*

by inhabiting sites with a long hydroperiods and having organic, peaty substrates. *Cyperus strigosus* typically occurs on seasonally wet mineral soils which are subject to acute drying in late summer months (personal observations). The relationship between *Cyperus strigosis* and *C. stenolepis*, both members of section *Strigosi*, has not previously been tested using molecular evidence. The null hypothesis is that these two species are closely related, as opposed to being morphologically similar due to convergence.

Problems in the Umbellati group

There are several focal taxonomic problems in *Cyperus* section Umbellati (C.B. Clarke) Kük. in Engler, *fide* Kükenthal (1935-1936). Since this section name is illegitimate and no legitimate name exists (Reynders et al. 2011), it will be referred to herein as the Umbellati group. This apparently artificial group (Reid et al. 2014) is diagnosed by the following traits: perennial duration, cormose plant bases, simple (unbranched) spikes, and spikelets usually possessing only one or two floral scales (Kükenthal 1935-1936). The taxonomic and nomenclatural histories of some taxa within this group are complex. The goals of this study relative to members of this group are to provide additional evidence for taxonomic evaluations, and to elucidate relationships. Focal Umbellati taxa in this research are *Cyperus blodgetii*, *C. echinatus*, and *C. retrorsus*.

Emphasizing similarities in floral scale posture and general inflorescence architecture, Carter (1984) relegated plants with dense spikes, ascending scales, and divaricate to reflexed primary inflorescence bracts to *Cyperus ovatus*. These plants were treated variously by Kükenthal (1935-1936) and Horvat (1941) as *Cyperus blodgettii*, *C. pollardii* Britton ex Small, *C. retrorsus* var. *curtisii* (C.B. Clarke) Kük., and *C. winkleri* Britton ex Small. Plants called *Cyperus blodgettii*, having greenish to reddish brown floral scales and fewer pedunculate spikes and primary inflorescence bracts, and being endemic to southern peninsular Florida, U.S.A., were provisionally given infraspecific rank under *C. ovatus* (Carter 1984). Desiring further study, Carter never published this new combination. *Cyperus blodgettii* was not accounted for by Tucker et al. (2002) in their *Flora of North America* treatment of *Cyperus*. This species is treated as a synonym of *C. retrorsus* by Govaerts et al. (2016). The null prediction is that *Cyperus blodgettii* is more closely related to *C. ovatus* than *C. retrorsus*.

Carter and Kral (1990) determined that *Cyperus echinatus* was the correct name for *C. ovularis* (Michx.) Torr. *Cyperus echinatus*, which is endemic to eastern North America, is easily recognized by its dense, spherical spikes (Carter 1984). Kükenthal (1935-1936) treated *Cyperus ovularis* (Michx.) Torr. var. *sphaericus* Boeckeler as a distinct taxon characterized by fewer and shorter rays, shorter spikelets, and more intensely reddish pigmented floral scales than the nominal variety now called *C. echinatus*. This variety was regarded by Carter (1984) as an ecotype not warranting formal rank. No combination has been published including "*sphaericus*" as an infraspecific taxon under *Cyperus echinatus*. Additional morphological evidence (Carter, unpublished data) has prompted re-evaluation of "*sphaericus*". Ecological evidence also suggests that "*sphaericus*" warrants formal naming. Whereas typical *Cyperus echinatus* tends to grow in disturbed areas on loamy and clayey soils, "*sphaericus*" occurs in sandy soils of high-quality, fire-maintained pine grasslands in the southeastern United States.

Cyperus retrorsus is nearly endemic to the Atlantic and Gulf of Mexico coastal plains of the southern and eastern United States. This species is a tufted perennial with cylindric spikes, and it grows in dry to mesic, often disturbed, sites. Several varieties of *Cyperus retrorsus* have been described, but these are often not recognized, with recent authors taking a broad view of *C. retrorsus* (e.g. Tucker et al. 2002,

Govaerts et al. 2016). *Cyperus retrorsus* var. *nashii* (Britt. ex Small) Fern. & Grisc. differs from the nominal variety by having spikes with less densely-packed spikelets, lustrous, fuscus floral scales with faint nerves, shorter anthers, broader and usually longer achenes, and smaller differences between floral scale lengths and achene lengths (Carter 1984). Ecologically, var. *nashii* is faithful to undisturbed xeric sand ridges, whereas var. *retrorsus* is a weedy element of more mesic soils. *Cyperus plankii* represents another species included in this study which is not typically recognized. Tucker et al. (2002) list this species as a synonym of *Cyperus croceus* while Govaerts et al. (2016) include it within *C. retorsus*. Also included in this study is an undescribed species, referred to herein as *Cyperus* sp. nov., which is hypothesized to be a close relative of *Cyperus retrorsus*. Like *Cyperus retrorsus* var. *nashii*, this entity occurs in undisturbed xeric sand ridges on the southeastern United States coastal plain. The goals of this study with respect to *Cyperus retrorsus* are to examine its taxonomy, using a molecular approach to determine whether a broad circumscription of this species is warranted, and to estimate the relationship of *Cyperus* sp. nov. to *C. retrorsus*.

Cyperus cephalanthus and the *C. rigens* group

Cyperus cephalanthus was first collected from coastal Texas in the southern United States and was described in 1836 (Torrey 1836). This sedge is now also known from wet coastal tall-grass prairies in Louisiana. Its relationship to similar plants in South America has long been suspected (Pedersen 1972) and was recently confirmed (Reid et al. 2014). In fact, specimens collected from humid grasslands in subtropical South America (Argentina, Brazil, and Paraguay) have been identified as *Cyperus cephalanthus*. *Cyperus cephalanthus* is most closely related to South American *C. impolitus* and *C. rigens.* Pedersen (1972) provided the most detailed taxonomic revision of the *Cyperus rigens* group, making several new combinations and providing a key to hypothetically related species. Pedersen (1972) treated *Cyperus cephalanthus* as a subspecies of *C. rigens* (*C. rigens* ssp. *cephalanthus* (Torr. & Hook.) T.M. Ped.). In Pedersen's key, *Cyperus cephalanthus* (*C. rigens* subsp. *cephalanthus*) keys out with taxa having nine nerves on the floral scales and being restricted to southeastern North America. Floral scales of North American *Cyperus cephalanthus* typically have seven nerves, and plants usually feature scabrous culm angles. Therefore, North American *Cyperus cephalanthus* key to *Cyperus impolitus* in Pedersen's treatment. Based strictly on morphology, *Cyperus cephalanthus* and *C. impolitus* may be indistinguishable. Hefler (2010) addressed the taxonomy of the *Cyperus rigens* group by lumping several *Cyperus rigens* subspecies, including subsp. *serrae*, which is included in this study, with *C. rigens* var. *rigens*. She also treated *Cyperus impolitus* as a variety of *C. rigens*, creating the new combination *C. rigens* var. *impolitus* (Kunth) Hefler & Longhi-Wagner (Hefler 2010). Hefler did not address *Cyperus cephalanthus*. Research goals are to elucidate relationships among the *Cyperus rigens* group and to determine if evidence shows molecular divergence of North American *Cyperus cephalanthus* from South American *Cyperus impolitus*.

Materials and Methods

Taxonomic sampling

Sampling of taxa for this study was guided mainly by the research goals described above. An attempt was also made to acquire samples of as many *Cyperus* species as possible during extensive field work. Most samples were collected by the author from the southeastern United States, Argentina, and Uruguay. Several samples were obtained from herbarium specimens and some were kindly provided by colleagues in other regions. Sequences for some ingroup and most outgroup taxa were obtained from

GenBank (www.ncbi.nlm.nih.gov). Taxon names, voucher specimen information, and GenBank accession numbers are supplied in Appendix 4. Scientific names are those accepted by Govaerts et al. (2016) in most cases. Alternative names are used to highlight taxa which may have merit, but that have been lumped with other taxa or not recognized, often without substantial evidence. For these taxa, names accepted by Govaerts et al. (2016) are also provided in Appendix 4. Most specimens are deposited at the Shirley C. Tucker Herbarium at Louisiana State University (LSU). Once databased and filed at LSU, specimen images can be viewed online at http://data.cyberfloralouisiana.com/lsu/. The herbarium code (Thiers continuously updated) is given only for specimens deposited elsewhere. Images of specimens deposited as VSC and FLAS can also be viewed online at http://herb.valdosta.edu/ database.php and https://www.flmnh.ufl.edu/herbarium/cat/catsearch.htm, respectively. To enable evaluation of biogeographic patterns, native ranges of taxa were determined by consulting Govaerts et al. (2016) and Kartesz (2015).

DNA extraction and marker amplification

Tissue samples were placed in silica gel upon collection in the field. Approximately 20 mg of dry leaf material was ground using the Mini-BeadBeater 8 (BioSpec Products, Bartlesville, OK, U.S.A.). Genomic DNA was extracted and purified using the DNeasy Plant Mini kit (Qiagen, Valencia, CA, U.S.A.) following manufacturer´s protocol. Amplifications were performed in 25 μl volumes containing 1 μl of template, 12.5 μl of Master AMP^{TM}, 0.5 μl of Tfl DNA Polymerase (Epicentre Biotechnologies), and 1 μl of each 10 nM forward and reverse primer.

Two chloroplast genes, two chloroplast intergenic spacers, and the nuclear ribosomal internal transcribed spacer were amplified. The gene *matK* was amplified using the forward primer *matK-1F* (5′-CGTCAACAACAATGCTTATATCC-3′) and the reverse primer *matK-5R* (5′-TTTATGT TTACGAGCCAAAG-3′) and the *ndhF* region was amplified using *ndhF-A* (5′-TATGGTTACC TGATGCCATGGA-3′) and *ndh-D1* (5′-CTATRTAACCR CGATTATATGAC CAA-3′) forward and reverse primers (Gilmour et al. 2013). Cycling conditions for amplification of *matK* and *ndhF* were as described in Gilmour et al. (2013). The intergenic spacers *rpl32-trnL*$^{(UAG)}$ and *trnH-psbA* were amplified using the primers and cycling conditions described in Shaw et al. (2007) (*trnL*$^{(UAG)}$: 5′-CTGCTTCCTAAGAGCAGCGT-3′, *rpL32-F*: 5′-CAGTTCCAAAAAAA CGTACTTC-3′, *Pe-trnH*: 5′-ATTCACAATCCACTGCCTTGAT-3′, *Pe-psbA*: 5′-AATGCACA CAACTTCCCTCTA-3′). Amplification of the nuclear internal transcribed spacer (*ITS*) (*ITS1-5.8S*rDNA-*ITS2*) followed the protocol described in Reid et al. (2014) using forward primer sef 17 (5'-ACGAATTCATGGTCCGGTGAAGTGT TCG-3') and reverse primer ser 26 (5'-TAGA ATTCCCCGGTTCGCTCGCCGTTAC-3') (Sun et al. 1994). Gel electrophoresis was performed to confirm success of PCR reactions. PCR products were shipped on dry ice to Beckman Coulter Genomics, Danvers, MA, U.S.A, for sequencing using the amplification primers. Returned sequences were subjected to a BLAST search (Altschul et al. 1990) to verify that the sequences belonged to the target organism and not a contaminant. Sequences were edited using Sequencher version 4.2.2 (Gene Codes Corporation). Multiple sequence alignments (MSA) of edited sequences were estimated with MAFFT version 7.017 (Katoh et al. 2002) using the MAFFT plug-in of Geneious version 6.1.5 (Drummond et al. 2010) using default settings (algorithm = auto; scoring matrix = 200PAM; gap open penalty = 1.53; offset value = 0.123).

Phylogenetic analyses

Phylogenetic hypotheses were inferred using Bayesian (BI) and Maximum Likelihood (ML) approaches. For BI analyses, the best-fit model of nucleotide sequence evolution was selected for each marker using MrModeltest version 2.3 (Nylander 2004). The best-fit model of nucleotide sequence evolution for ML analysis was selected using jModelTest version 2.1.7 (Darriba et al. 2012). For BI analysis, models selected under the Akaike Information Criterion (AIC) were GTR+G for all markers except for 5.8SrDNA, for which SYM+I+G was selected. For ML analysis, models selected using the corrected Akaike Information Criterion (AICc) were K80+G for ITS1, TIM3ef+I+G for 5.8SrDNA, K80+G for ITS2, TNM+I+G for *matK*, TPM3uf+I+G for *ndhF*, TVM+G for *rpl32-trnL*$^{(UAG)}$, and TIM3+G for *trnH-psbA*.

Bayesian analyses were conducted using MrBayes version 3.1.2 (Ronquist & Huelsenbeck 2003) via the CIPRES Science Gateway (Miller et al. 2010) and ML analyses were performed using Garli version 2.01 (Zwickl 2006) for independent locus and concatenated MSAs. The number of sequences of individual regions varied based on variable success of PCR reactions preformed for this research and availability of sequences from GenBank. Missing data is indicated in Appendix 4. Following confirmation of general agreement among single locus trees, concatenated MSAs including all five loci and only the four plastid loci were assembled using SequenceMatrix version 1.8 (Gaurav et al. 2011) with partitions corresponding to individual loci. To be included in the concatenated MSA containing all five markers, a taxon had to have sequences available for at least three out of five loci with ITS data present, or four out of five loci when the ITS sequence was lacking. Taxa having data present for at least two of the four plastid regions were admitted into the plastid concatenated MSA.

The BI analysis of the five-marker concatenated MSA consisted of four parallel runs using one heated (temp=0.1) and three cold chains per run for 20,000,000 generations, sampling every 2,000 generations. Bayesian analysis of the plastid MSA used the same parameters except that sampling frequency was every 1,000 generations. Models of sequence evolution selected by MrModeltest were applied to each partition, which corresponded to individual genic loci. All parameters of sequence evolution were unlinked across partitions. Convergence of each run was assessed by ensuring that potential scale reduction factors (PSRF) reported in MrBayes were close to 1 and effective sample size (ESS) values were greater than 200 in Tracer version 1.5 (Rambaut et al. 2014). Bayesian majority-rule consensus trees for five-locus and plastid concatenated MSAs were produced from stationary distributions after discarding the first 25% of sampled trees as burn-in.

The ML analyses of the partitioned concatenated MSAs were estimated from 20 replicate searches for the best tree with a starting tree generated by stepwise addition with fifty attachments evaluated per taxon and twenty independent search replicates per dataset. If the best tree with the same topology was not found more than once across twenty search replicates, the number of search replicates was increased to 100. For both concatenated MSAs, node support was estimated from ML analysis of 1008 pseudoreplicate bootstrapped datasets with the best tree from two search replicates stored per bootstrap dataset for the calculation of node frequencies. Support values (both posterior probabilities and node frequencies) were mapped onto the ML trees with SumTrees version 3.3.1 using the DendroPy Phylogenetic Computing Library version 3.12.0 (Sukumaran & Holder 2010). The final trees were inspected in FigTree version 1.4.2 (Rambaut 2006-2009) and prepared for publication using Adobe® Illustrator® CC and Photoshop® CS5.

Results

The results of individual-locus phylogenetic analyses showed considerable variation in resolution across the five molecular markers; however, they were generally congruent. The five-locus concatenated MSA included 122 ingroup and 13 outgroup taxa. The aligned concatenated five-marker matrix, consisting of seven partitions corresponding to individual loci (ITS containing three partitions), had a total of 5,921 characters. Despite 100 ML search replicates, the best tree was not found more than once. The phylogenetic tree resulting from the five-marker concatenated analysis is presented in Figures 4 and 5. Outgroup taxa *Fuirena robusta* Kunth, *Schoenoplectus lacustris* (L.) Palla, *S. tabernaemontani* (C.C. Gmel.) Palla, and *Scleria verticillata* Muhl. ex Willd. were pruned from the final tree using Mesquite version 3.04 (Maddison & Maddison 2015) to reduce compression of branches. The plastid concatenated matrix included 125 ingroup and 16 outgroup taxa. The aligned concatenated plastid matrix had four partitions and a total 5,196 characters. In the analysis of the plastid MSA, the best ML tree was found more than once in 20 search replicates. The same outgroup taxa pruned from the five-marker phylogenetic tree plus *Calliscirpus brachythrix* C.N. Gilmour, J.R. Starr, & Naczi and *Scleria muehlenbergii* Steud., were similarly pruned from the plastid tree, which is presented in Figures 6 and 7.

Discussion

This discussion is relative to the five-marker phylogenetic analysis and the resulting hypothesis presented in Figures 4 and 5; this is the most robust result generated from this research. The plastid tree (Figures 6 and 7) was estimated to admit *Cyperus schoburgkianus* in this study. Material of this species was not available for DNA extraction. It is included on the basis of *rpl32-trnL*$^{(UAG)}$ and *trnH-psbA* sequences available from GenBank, which were not adequate to permit inclusion of this taxon in the five-marker analysis.

Cyperus is monophyletic and strongly supported (bootstrap proportion (bsp)/posterior probability (pp) = 100/1.00) (Figure 4). Taxa possessing C_3 photosynthesis form a grade (Figure 4) that is basal to a C_4 clade (bsp/pp = 100/1.00) (Figure 5). As with other studies (Larridon et al. 2013, Reid et al. 2014), the C_4 clade is poorly resolved at deeper nodes and branch lengths are short. Resolution in the C_4 clade improves toward branch tips in some cases, with smaller clades representing hypothetically closely related species.

Several C_3 clades (Figure 4) correspond to taxonomic sections within *Cyperus* (Kükenthal 1935-1936; Larridon et al. 2011c) and are so labeled. Clades correspond to sections *Haspani* (Kunth) C.B. Clark, *Fusci* (Kunth) C.B. Clarke, *Oxycaryum* (Nees) Larridon (Larridon et al. 2011c) and *Luzuloidei* (Kunth) C.B. Clarke (Figure 4). Results support the inclusion of *Cyperus incomtus* within section *Luzuloidei*, as suggested in Larridon et al. (2011c). Included in section *Luzuloidei* by Kükenthal (1935-1936), this species was excluded from a taxonomic study of the *Luzulae* group by Denton (1978) because of her opinion that it belonged in section *Elegantes* C.B. Clarke (sect. *Glutinosi* Boeckeler sensu Kükenthal (1935-1936)). This study included five members of section *Luzuloidei* (*Cyperus acuminatus, C. incomtus*, *C. intricatus*, *C. reflexus*, and *C. virens*) that were not included in the phylogenetic analysis of Larridon et al. (2011c), increasing the confidence that this group is monophyletic.

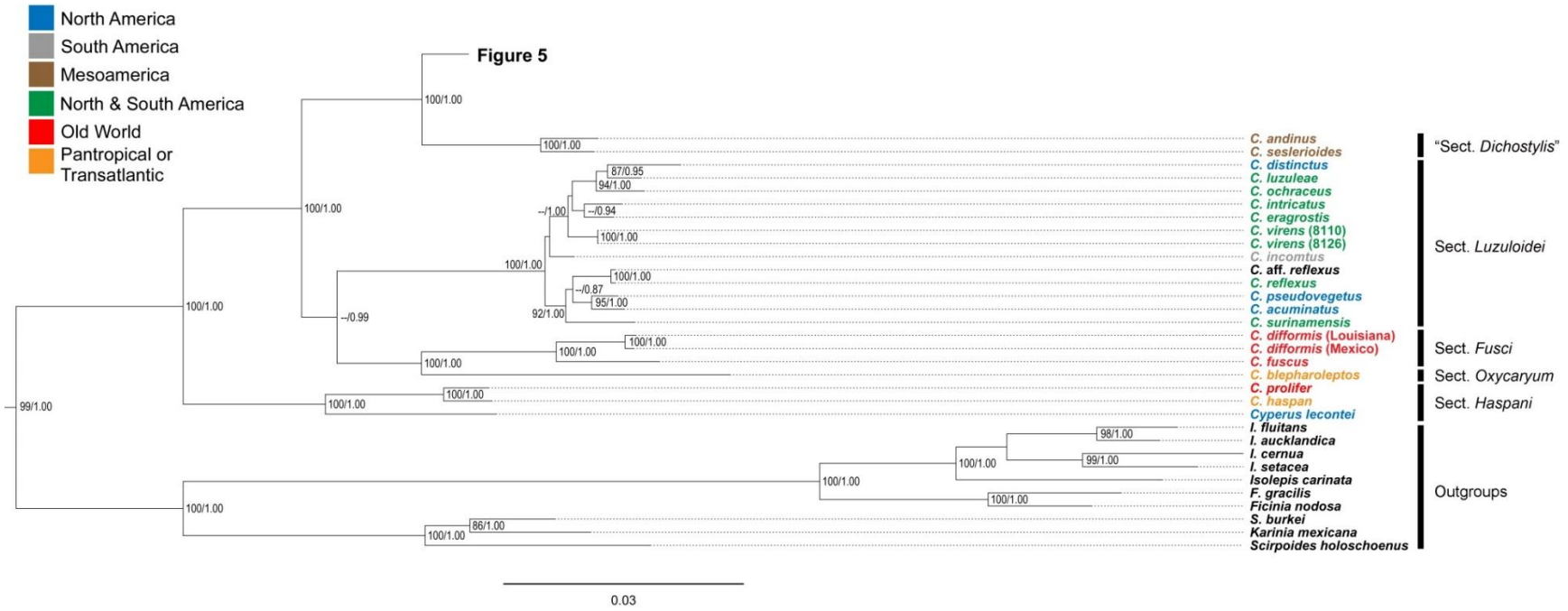

Figure 4. Outgroups and *Cyperus* C_3 grade. Maximum likelihood tree inferred from a concatenated multiple sequence alignment (MSA) consisting of sequences from nuclear *ITS*, and plastid markers *matK*, *ndhF*, *rpl32-trnL*, and *trnH-psbA*. Node support values are given when ML bootstrap proportion is ≥ 70 or BI posterior probability is ≥ 0.85. Font color of taxon names corresponds to the taxon's native center of distribution according to the legend.

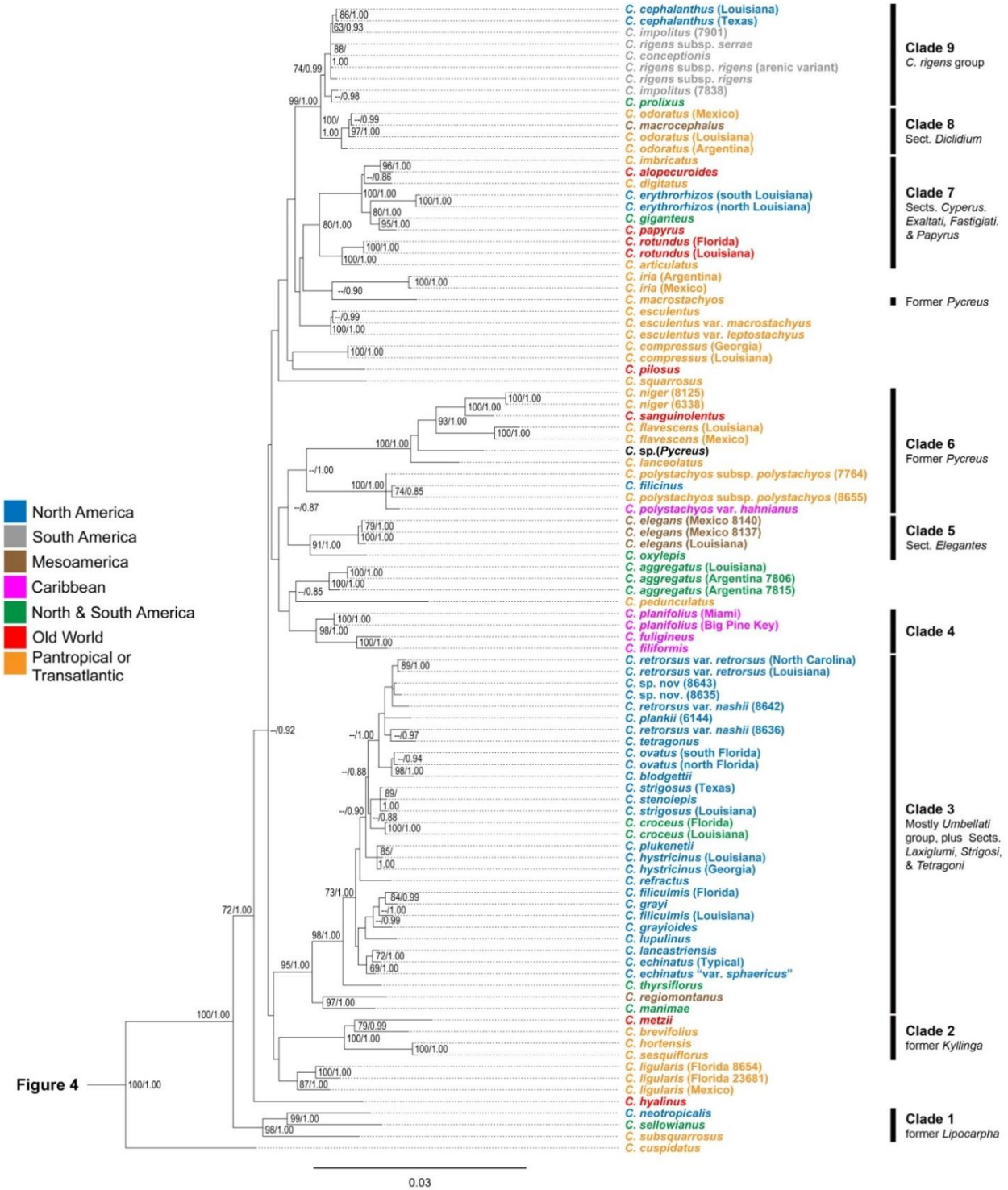

Figure 4

Figure 5. *Cyperus* C_4 clade. Maximum likelihood tree inferred from a concatenated multiple sequence alignment (MSA) consisting of sequences from nuclear *ITS*, and plastid markers *matK*, *ndhF*, *rpl32-trnL*, and *trnH-psbA*. Node support values are given when ML bootstrap proportion is ≥ 70 or BI posterior probability is ≥ 0.85. Font color of taxon names corresponds to the taxon's native center of distribution according to the legend.

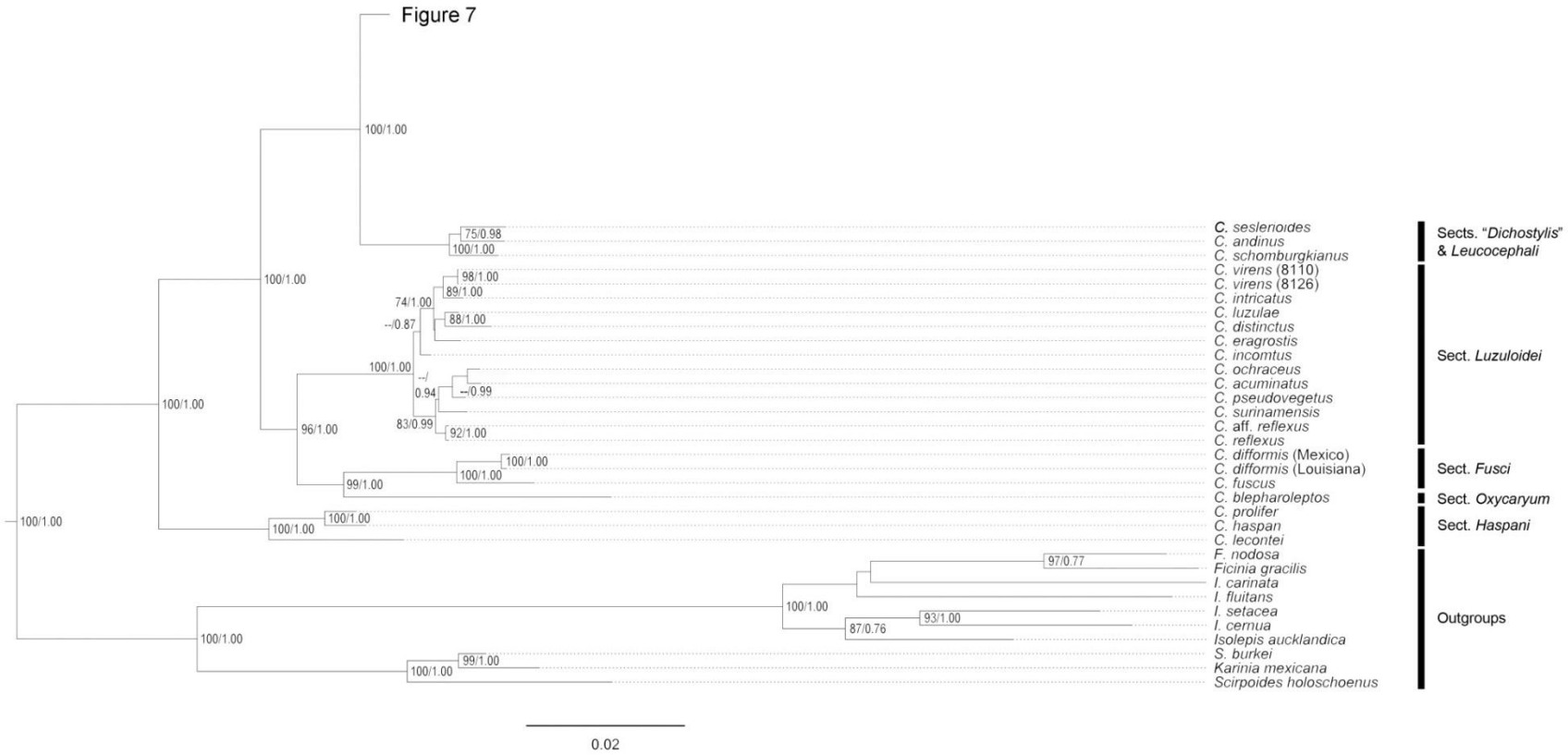

Figure 6. Outgroups and *Cyperus* C_3 grade. Maximum likelihood tree inferred from a concatenated MSA consisting of plastid markers *matK*, *ndhF*, *rpl32-trnL*, and *trnH-psbA*. Node support values are given when ML bootstrap proportion is ≥ 70 or BI posterior probability is ≥ 0.85.

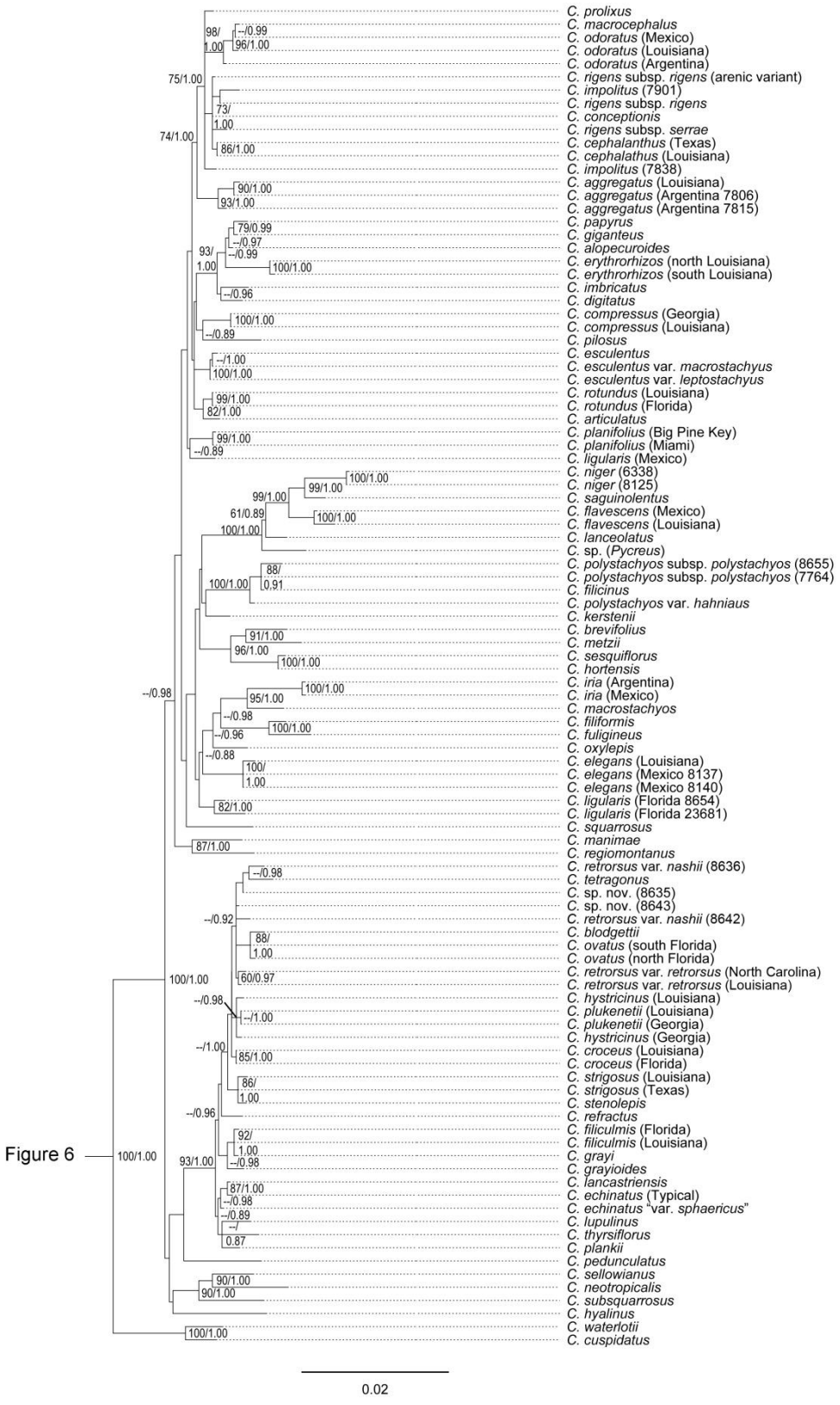

Figure 6

Figure 7. *Cyperus* C_4 clade. Maximum likelihood tree inferred from a concatenated MSA consisting of sequences from the plastid markers *matK*, *ndhF*, *rpl32-trnL*, and *trnH-psbA*. Node support values are given when ML bootstrap proportion is ≥ 70 or BI posterior probability is ≥ 0.85.

Within the C_4 clade, *Cyperus cuspidatus* is sister to the remaining taxa in this clade (Figure 5), a phylogenetic position consistently inferred in previous studies (Muasya et al. 2001, 2002, Larridon et al. 2011c, Reid et al. 2014). The phylogenetic position of *Cyperus hyalinus* (*Queenslandiella hyalina*) as sister to the large *C. ligularis* L. -- *C. cephalanthus* clade containing the vast majority of C_4 taxa has fairly strong support (bsp/pp = 72/1.00; Figure 5). Taxa formerly included in the genus *Lipocarpha* R. Br. compose Clade 1. *Cyperus subsquarrosus* (formerly *Lipocarpha micrantha* and *Hemicarpha micrantha* (Vahl) Pax) is a member of the newly erected *Cyperus* section *Neohemicarpha* Bauters (Bauters et al. 2014). *Cyperus neotropicalis* and *C. sellowianus* are placed in *Cyperus* section *Lipocarpha* (Bauters et al. 2014). Clade 2 includes species formerly of the genus *Kyllinga*. Clade 6 includes species formerly treated as *Pycreus* P. Beauv. *Cyperus macrostachyos*, also formerly in *Pycreus*, is well-removed from other former *Pycreus* (Figure 5).

Clade 7 (Figure 5) includes members of five sections, as employed by Kükenthal (1935-1936): *Brevioliati* C.B. Clarke (nom. illeg., cf. Larridon et al. 2011c), *Exaltati* (Kunth) C.B. Clarke, *Fastigiati* Kük., *Papyrus* (Willd.) Thouars, and *Rotundi* C.B. Clarke (= sect. *Cyperus*, cf. Larridon et al. 2011a). These groups share long or medium length styles and winged rachillas (Kükenthal 1935-1936). *Cyperus articulatus* and *C. rotundus* form a sub-clade within Clade 7. The gestalt morphological similarity between these two species is striking.

Phylogenetic Position of *Karinia*

This study is the first to estimate the phylogenetic position of *Karinia*, a monotypic genus endemic to Mexico. *Karinia* is nested within *Scirpoides* Ség. with strong support (Outgroups, Figure 4). *Scirpoides* has seven species and subspecific taxa and is distributed in the Old World from southern Africa to Europe and Eurasia (Govaerts et al. 2016). A specimen of *Karinia mexicana* failed to key to *Scirpoides* using Goetghebeur's (1998) generic key mainly because this species has terminal rather than pseudolateral inflorescences. However, other aspects of the morphology of *Karinia*, including a tenacious perennial habit, capitate inflorescence with numerous spikelets, and spirally-arranged floral scales having many parallel nerves, fit the diagnosis of *Scirpoides*. Goetghebeur (1998) tentatively combined *Karinia* with *Scirpoides* stating that additional information was needed to confirm such placement. Molecular evidence supports transfer of *Karinia mexicana* to genus *Sciproides*.

Closest Relatives of C_4 *Cyperus*

In the phylogenetic tree based on analysis of all five molecular makers, *Cyperus seslerioides* and *C. andinus* are resolved as sister to C_4 *Cyperus* (Figure 4). While they are lumped nowadays, the samples of these two taxa used in this study differ markedly in floral scale color, venation, and size, and in achene size, shape, and surface texture. Whether *Cyperus andinus* should be resurrected is beyond the scope of this study. The taxonomic status of this specis is currently being addressed by other workers (Socorro Gonzalez, personal communication). Lack of sequences did not permit *Cyperus schomburgkianus* from being included in the five-marker analysis. However, *Cyperus schomburgkianus* was included in the analysis of four plastid markers.

Figure 8. *Cyperus seslerioides* in Arizona, U.S.A. Photo by Max Licher, Northern Arizona University. Used with permission.

The plastid tree includes *Cyperus andinus*, *C. schomburgkianus*, and *C. sesslerioides*; these three taxa resolve together in a well-supported clade that is sister to C_4 *Cyperus* (Figure 6). Phylogentic anlaysis of the ITS region in this study resolved a strong relationship between *Cyperus pulchellus* R.Br., an Old World tropical member of section *Leucocephali* (Simpson 1990) and *C. andinus* (bsp/pp=75/1.00; tree not pictured).

Figure 9. *Cyperus schomburgkianus* in State of Minas Gerais, Brazil. Photo by William Milliken, RBG/Kew. Used with permission.

Simpson (1990) observed that *Cyperus seslerioides* superficially resembled *C. tenerrimus* J. Presl & C. Presl, a member of section *Leucocephali*, but noted that *C. seslerioides* differed from members of section *Leucocephali* by the combination of having outward curving (versus inrolled) floral scale margins, excurrent scale apices and ellipsoidal (versus shortly cylindrical to globose) achene shape. Considering the phylogentic results presented herein and the range of variation in Simpon's (1990) sectional description of *Leucocephali*, assignment of *C. seslerioides* and *C. andinus* to section *Leucocephali* would likely not be noncontroversial. Other C_3 members of "section *Dichostylis*" such as *Cyperus humilis* Kunth, *C. microbrunneus* G.C. Tucker, and *C. uncinulatus* Schrad. ex Nees should be subjects for molecular studies in the near future. As with *Cyperus seslerioides* and *C. andinus*, and currently recognized members of section *Leucocephali*, they possess spherical to hemispherical inflorescences and occupy upland habitats (Figures 8 and 9) (Tucker 1994).

Cyperus section *Diclidium*

Three species of section *Diclidium* were included in this study: *Cyperus filiformis*, *C. macrocephalus*, and *C. odoratus*. *Cyperus macrocephalus* is considered synonymous with *C. odoratus* by some (Tucker 1994, Govaerts et al. 2016) and recognized as distinct by others (Adams 1994 as *Torulinium macrocephalum* (Liebm.) C.B. Clarke, Jones et al. 1996). *Cyperus macrocephalus* and *C. odoratus* compose Clade 8 (Figure 5), while *C. filiformis* is well-removed, being placed in a strongly supported sister relationship with *C. fuligineus* (Clade 4, Figure 5). Therefore, section *Diclidium* is polyphyletic. In addition to *Cyperus filiformis*, Clade 4 contains *C. planifolius* and *C. fuligineus* which belong to sections *Thunbergiani* (C.B. Clarke) Kük. and *Laxiglumi* (C.B. Clarke) Kük., respectively. Section *Thunbergiani* is also represented by *Cyperus cephalanthus*, *C. impolitus*, and *C. rigens* in Clade 9 (Figure 5). Additonal representatives of section *Laxiglumi* include *Cyperus filiculmis*, *C. grayi*, *C. grayioides*, and *C. lupulinus* which fall in Clade 3. Sections *Thunbergiani* and *Laxiglumi* are polyphyletic based on these results (Figure 5). While Clade 4 does not give credence to an existing classification, its members are geographically similar in having Caribbean distributions (Figure 5).

Cyperus odoratus (Clade 8) is only distantly related to *C. pedunculatus*, which occurs in a clade that is sister to Clade 4 (Figure 5). This result would seem to indicate two independent origins of the corky rachilla. However, while Clade 8 is strongly supported as sister to the *Cyperus rigens* group (Clade 9, Figure 5), the phylogenetic placement of *C. pedunculatus* is not strongly supported. Given the weak support along the backbone of the tree, the hypothesis that *C. pedunculatus* is sister to the lineage that includes clades 8 and 9 cannot be rejected. This placement would suggest a single gain of the corky rachilla followed by one or more losses. More complete taxon sampling and more informative sequence data are needed to address this hypothesis.

Cyperus stenolepis and *C. strigosis*

Cyperus stenolepis and *C. strigosis* form a well-supported clade nested within Clade 3 (Figure 5). There is evidently little divergence in the molecular markers employed in this study between samples representing these taxa. The phylogenetic hypotheses presented in Figures 5 and 7 support classifications which treat *Cyperus stenolepis* as a synonym of *C. strigosis* (Govaerts et al. 2016, Tucker et al. 2002). An analysis including more samples of these taxa and employing different

molecular markers may yield different results. Until a more intensive analysis is performed, *Cyperus stenolepis* is best treated as a variety of *C. strigosis* considering results presented here and morphological and ecological traits.

Taxonomic Insights in the *Umbellati* Group

Most of the taxa in Clade 3 (Figure 5) are members of the *Umbellati* group. This group is paraphyletic since Clade 3 also includes members of sections *Laxiglumi, Strigosi*., and *Tetragoni* Kük. Specific goals of this research were to gain greater understanding of *Cyperus blodgettii*, *C. echinatus*, and *C. retrorsus*.

This phylogenetic analysis, which included samples of *Cyperus ovatus* from northern and southern Florida, shows a sister relationship between *C. ovatus* and *C. blodgettii* (Clade 3, Figure 5). This result supports a relationship between *Cyperus blodgettii* and *C. ovatus* as suspected by Carter (1984) based on detailed morphological study and supports the treatment of *C. blodgettii* as a variety of *C. ovatus*. Additional support from a phylogenetic analysis including more samples of both taxa would be prudent prior to making this new combination.

Typical *Cyperus echinatus*, *C. echinatus* "*sphaericus*", and *C. lancastriensis* form a strongly-supported clade (Clade 3, Figure 5). A previous analysis by Reid et al. (2014) showed a well-supported sister relationship between *Cyperus echinatus* "*sphaericus*" and *C. filiculmis* (Clade F, Figure 3). The phylogenetic analysis presented herein does not resolve such a relationship, though *Cyperus filiculmis* is not far removed (Clade 3, Figure 5). The "*sphaericus*" variant has no legitimate name. Therefore, *Cyperus echinatus*, as currently circumscribed (Carter 1984, Carter and Kral 1990) is paraphyletic due to its phylogenetic position relative to *C. lancastriensis* and *C. echinatus* "*sphaericus*". Results of this analysis could be used in combination with morphological and ecological evidence (reviewed above) to support the treatment of "*sphaericus*" as a distinct taxon at the rank of species. A molecular study involving multiple samples of typical *Cyperus echinatus*, *C. echinatus* "*sphaericus*", and *C. lancastriensis* is warranted.

Cyperus retrorsus var. retrorsus, *C. retrorsus* var. *nashii*, *C. plankii*, *C.* sp. nov., and *C. tetragonus* Elliott form a weakly supported sub-clade (bsp/pp=32/0.82) nested within Clade 3 (Figure 5). With the exception of the sister relationship between with two *Cyperus retrorsus* var. *retrorsus* samples, node support values within this sub-clade are weak (Clade 3, Figure 5) suggesting these taxa are related but providing little confidence. The erratic placement of *Cyperus retrorsus* var. *nashii* may be due to lack of ITS sequences for both samples of this taxon (Appendix 4). The ITS region was the most informative molecular marker based on inspection of single-marker trees. Since DNA sequences employed thus far have provided little resolution between *Cyperus retrorsus* and often-included taxa, morphological and ecological evidence should be given more weight in taxonomic decisions involving *C. retrorsus* and its segregates and hypothetical relatives.

Relationships and Biogeography of the *Cyperus rigens* group

The *Cyperus rigens* group, including *C. cephalanthus*, *C. impolitus*, *C. prolixus*, and two subspecies of *C. rigens*, is monophyletic with strong support (Clade 9, Figure 5). The two *Cyperus cephalanthus* samples have a strongly-supported sister relationship and are sister to *C. impolitus* (7901) with moderate support (Clade 9, Figure 5). The other *Cyperus impolitus* sample (7838) is well-removed, resolved as sister to *C. prolixus*. Poor resolution within Clade 9 is likely due to very little sequence variation. More informative molecular data and more intensive sampling are required to assess relationships in the *Cyperus rigens* group and to test for divergence between *C. cephalanthus* and its South American relatives.

While relationships are still unclear within the *Cyperus rigens* group, results strengthen support for an amphitropical disjunction within this group. Tucker et al. (2002) suggested that *Cyperus cephalanthus* is naturalized rather than native to North America. Since *Cyperus cephalanthus* was collected and described early in the colonization of the southern United States and is a conservative component of coastal tall-grass prairies (Carter & McInnis 1993, Grace et al. 2000, Allain et al. 2004), it is most likely native to the northern Gulf of Mexico coast rather than a recent anthropic introduction. Sedges have small fruits and are known to disperse long distances (Kern 1974). Fruits embedded in mud can adhere to birds' feet, or become lodged in their feathers (Darwin 1859; Ridley 1930). Raven (1963) noted that amphitropical disjuncts between North and South America correspond closely to bird migration routes and that these species tend to occur in open habitats, such as coastal and wetland communities. Rosen (2007) reported 10 amphitropical disjuncts, in addition to *Cyperus cephalanthus*, in his floristic study of a high-quality coastal prairie remnant in southeastern Texas. There are many avian candidates that may have served as vectors for *Cyperus cephalanthus*. The presence of this species in North America could have resulted from one dispersal event, several, or many, depending on the probability of the dispersal mode. Since the once-extensive coastal prairie habitat of *Cyperus cephalanthus* in Louisiana and Texas has been reduced to less than 1% of its historical extent (Smeins et al 1991, Holcomb et al. 2015), it is likely that this species is now effectively isolated from gene flow from South America.

Biogeographical Observations

This phylogenetic analysis includes ca. 10 % of the known species in *Cyperus*. Sampling intensity is inadequate to rigorously examine biogeographic patterns. However, it does present some preliminary biogeographic insights. The overwhelming majority of North American endemics sampled fall in Clade 3 (Figure 5). *Cyperus regiomontanus* and *C. manimae*, which are sister to the remainder of Clade 3, have more southerly distributions, occurring in Mexico and Central America and extending into tropical South America. *Cyperus thyrsiflorus* is also more southerly, being present in subtropical North America and extending into tropical America. From the phylogenetic hypothesis presented in Figure 5, it is possible that many North American endemics were derived from a more southern ancestor. Clade 3, consisting of mostly North American endemics and many species of decidedly upland habitats, may represent a natural radiation. Future studies including more taxa are needed to continue examination of this possibility.

Conclusions

This research made several contributions to the body of knowledge regarding the systematics of *Cyperus* and Cyperaceae. The position of *Karinia* was resolved with confidence; the only species in this genus, *K. mexicana*, should be transferred to *Scirpoides*. This research provides evidence that *Cyperus seslerioides* and *C. andinus* are closely related to members of section *Leucocephali*, and that these species are sister to C_4 Cyperus. Sampling additional members of section *Leucocephali* and providing a taxonomic revision of this group that is informed by molecular evidence should be near-term priorities for the *Cyperus* research community. Several taxonomic problems were addressed with some satisfaction among North American C_4 taxa (Clade 3). In all cases, a greater number of samples and more informative molecular data are needed to increase confidence. This work provided strong evidence of the amphitropical disjunction within the *Cyperus rigens* complex. Lack of sequence variation hindered the generation of a well-resolved phylogenetic hypothesis among taxa within that group. *Cyperus cephalanthus* is a species of conservation concern in North America (Holcomb et al. 2015, NatureServe 2015). Genetic data yielding meaningful variation at the population level are needed to test for divergence between North America and relatives in South America and to examine genetic diversity within northern Gulf of Mexico *Cyperus cephalanthus* populations. Such studies may garner evidence supporting evolutionary independence and rarity of *Cyperus cephalanthus*, elevating it as a conservation priority.

CHAPTER 4.
MORPHOMETRIC ANALYSIS OF THE *CYPERUS RIGENS* SPECIES GROUP

Introduction

The *Cyperus rigens* complex is a confusing group concentrated in subtropical South America. One member, *Cyperus cephalanthus*, occurs in subtropical North America along the northern Gulf of Mexico coast. The problems in this group stem from some early taxonomic errors, the nature of the practice of taxonomy in the 18ths and 19th centuries with respect to communication (many superfluous names), and, especially, complex morphological variation.

Pederson (1972) was the first author to address problems in this group by reviewing the taxonomy and nomenclatural history of *Cyperus laetus* and *C. rigens*. He examined the type specimens of *C. laetus* and *C. rigens* and determined that the original concept of *C. laetus* was supplanted by a concept actually based on *C. rigens*. In other words, the names had been reciprocally misapplied. Several workers including Kunth and Nees von Esenbeck modified the concept of *C. laetus* to fit additional material without seeing authentic material of *C. laetus* (Pedersen 1972). The erroneous concept of *Cyperus laetus* was adopted by Kükenthal (1935-1936). As Pederson discovered by examining type material, *C. laetus* looks nothing like *C. rigens*. *Cyperus laetus* has deep red floral scales, unlike *C. rigens*, and the range of *C. laetus* lies to the north of the range of *C. rigens*. Pedersen (1972) recognized the following taxa: *Cyperus laetus*, *Cyperus rigens* subsp. *rigens* var. *rigens*, *C. rigens* subsp. *rigens* var. *capitatus* Presl, *C. rigens* subsp. *rigens* var. *maximus* (Kükth.) T.M. Ped., *C. rigens* subsp. *rigens* var. *selmirae* T.M. Ped., *C. rigens* subsp. *cephalanthus* (Torr. & Hook.) T.M. Ped., *C. rigens* subsp. *arechavaletae* (Boeckeler) T.M. Ped., *C. rigens* subsp. *serrae* (Bcklr.) T.M. Ped., *C. impolitus* Kunth, *C. tacnensis* Nees & Meyen var. *tacnensis*, *C. tacnensis* var. *weberbaueri* (Kük.) T.M. Pedersen, *C. tacnensis* var. *tarijensis* (Kükth.) T.M. Ped., and *C. grossianus* T.M. Ped. Pederson's treatment includes synonomy and a dichotomous key but no species descriptions.

The study presented here was stimulated by the amphitropical disjunction of *Cyperus cephalanthus* and the desire to determine its relationship to South American relatives. *Cyperus cephalanthus* was described from material collected at Galveston Bay, in the coastal prairie region of southeastern Texas (Torrey 1836). Kükenthal (1935-1936) treated *C. cephalanthus* as a variety of *C. laetus*, but his identification of *C. laetus* was incorrect (Pedersen 1972). Recent North American botanical works such as those of Thomas and Allen (1993), Jones et al. (1997), and Tucker et al. (2002) use the name *Cyperus cephalanthus* rather than the combination proposed by Pedersen (1972). *Cyperus cephalanthus* is a species of conservation concern in Louisiana and Texas (Holcomb et al. 2015, NatureServe 2015). Only two extant populations are known from Texas (Rosen and Christoffersen 2004; David Rosen, personal communication) while 14 records are known from Louisiana (Louisiana Natural Heritage Program, unpublished data). All North American records of *Cyperus cephalanthus* are from wet coastal tall-grass prairie remnants. This species does not occur as a weed in various types of disturbed wetlands, as do many exotic and native *Cyperus* species in the region. Examination of herbarium specimens from South America and field observations by the author in Argentina reveal that *Cyperus cephalanthus* is very similar to the South American *Cyperus impolitus*. Based on similarity to specimens from South America, Tucker et al. (2002) also included Argentina, Brazil, Paraguay, and Uruguay in the distribution of *Cyperus cephalanthus*. Govaerts et al. (2016) include Argentina, Paraguay, and Uruguay, in addition to Louisiana and Texas, in the range of *Cyperus cephalanthus.*

Pedersen's (1972) treatment has some inconsistencies and ambiguities. For example, Pedersen cites the presence of scabrous stem angles in *C. impolitus* among the characters useful in distinguishing it from *C. rigens*. However, he included within *C. rigens* several infraspecific taxa, including subsp. *cephalanthus*, that have scabrous stem angles as well, thus creating confusion. In his key, Pedersen (1972) also distinguishes *Cyperus laetus* from *C. rigens* (incl. *C. r.* subsp. *cephalanthus*) based upon persistent spikelets, despite the fact that some North American specimens of *C. cephalanthus* exhibit this condition as well. Pederson (1972) heavily weights number of nerves present on floral scales, with *C. cephalanthus* (*C. rigens* ssp. *cephalanthus*) keying as having 9-nerved scales, although scales of North American material of *C. cephalanthus* are predominantly 7-nerved. Thus, in Pedersen's treatment, North American *Cyperus cephalanthus* specimens usually key to *C. impolitus*.

Some taxonomic changes in the *Cyperus rigens* group were recently proposed by Hefler (2010). Based on morphological continuity, Hefler (2010) treated the taxa *Cyperus rigens* subsp. *rigens* var. *capitatus*, *C. rigens* subsp. *serrae*, *C. rigens* ssp. *rigens* var. *maximus*, and *C. rigens* subsp. *rigens* var. *selmirae* as synonyms of *C. rigens* var. *rigens*. She also proposed the new combination *C. rigens* var. *impolitus* (Kunth) Hefler & Longhi-Wagner, reducing *C. impolitus* to a variety of *C. rigens*. Hefler did not address *C. cephalanthus* (*C. rigens* ssp. *cephalanthus*). The taxonomic changes proposed by Hefler (2010) followed extensive herbarium review of specimens for her dissertation project, a floristic treatment of *Cyperus* subgen. *Cyperus* of southern Brazil (Hefler 2007, not acquired by author). An important component of her work was extensive field observations, at least in Brazil, allowing her to make decisions after observing variation between populations.

There are currently no taxonomic references which allow *Cyperus cephalanthus* and *C. impolitus* to be distinguished based on morphology. Molecular divergence between these two taxa and among the *Cyperus rigens* group is negligible (Chapter 3 of this dissertation). The primary goal of this research is to determine if North American *Cyperus cephalanthus* is morphologically separable from South American *Cyperus impolitus*. While the author conducted field work in Argentina and Uruguay during this research, his field observations were not extensive enough to address the large amount of morphological and ecological variation among *Cyperus rigens* and its infraspecific taxa. With repsect to *Cyperus rigens*, this study is only preliminary, pending more extensive field work in South America.

Materials and Methods

Specimens representing the *Cyperus rigens* group were borrowed from herbaria in North and South America. Based on completeness and degree of maturity, 133 specimens (Appendix 3) were selected for morphopmetric study using principal components analysis (PCA), implemented with Statistical Analyis System (SAS) version 9.4. Data from 61 characters were recorded (Table 1). Microscopic variables and angles were measured using the cellSens™ microscope imaging softerware (Olympus Corporation). The characters measured are those typically included in detailed taxonomic descriptions. Operational Taxonomic Units (OTUs) represented in the PCA studies are listed in Table 2. An initial PCA included all 133 taxa and 61 characters measured from specimens (Table 1). Following the initial PCA run, strongly correlated ($r \geq 0.90$) characters pairs were assessed and one character from each pair was removed. Anther length (ANTHLEN) was removed due to excessive missing data. A second PCA included 47 characters; characters removed based on the correlation matrix are noted in Table 1. After inspecting the results of the PCA based on all measured characters minus select characters involved in

correlations, it was determined that using such an exhaustive list of variables, some of which are surely subject to plasticity, was not informative. The number of characters was reduced to 13 (Table 1).

Table 1. Characters measured in the morphometric study of the *Cyperus rigens* species group. Characters eliminated from the 61-variable PCA based on degree of correlation with other characters or for other reasons are noted with an asterisk (*). Thirteen characters used in a reduced PCA analysis are followed by a superscript "R" (^{R}).

Character	Description
CULMHT^{R}	culm height from base of plant to base of anthelum (cm)
CULMWB	culm width 2 cm from base (mm)
CULMWM	culm width at midpoint (mm)
CULMWT	culm width 2 cm below anthelum (mm)
LTAPER*	lower taper: CULMWB - CULMWM (mm)
MTAPER	upper taper: CULMWM - CULMWT (mm)
TTAPER*	total taper: CULMWB minus CULMWT
SCABROS^{R}	culm scabrosity: number of teeth on culm angle in 1 cm stretch centered 2 cm below anthelum
SCABPA	culm scabrosity: presence/absence
LEAFNUM	total number of leaves
LEAFSCALE	number of scale leaves
LEAFRED	number of reduced narrow-bladed leaves
BLADEW	maximum blade width (mm)
BRACTNUM1	total bract number
BRACTNUM2	number of anthelum bracts exceeding longest ray
BRACTNUM3	number of anthelum bracts exceeding anthelum
BRACTLEN	maximum anthelum bract length (cm)
BRACTW	maximum anthelum bract width (mm)
BRACTANG	angle of most divergent anthelum bract
RAYNUM	number of rays
RAYLEN	maximum ray length (cm)
ANTHLEN*	anthelum length (cm)
ANTHWID^{R}	anthelum width (cm)
SPIKENUM	total number of spikes
SPIKELEN	maximum spike length (mm)
SPIKEWID	maximum spike width (mm)
SPIKEDENS^{R}	spike density – number of floral scales visible within 5 sq. mm circular plot taken on a representative spike
SPKLTASC	spikelets at mid-spike ascending (presence/absence)
SPKLTSPR	spikelets at mid-spike spreading (presence/absence)
SPKLTLEN*	spikelet length (mm)
SPKLTW	spikelet width (mm)
SCALENUM	total number of floral scales on a representative spikelet
FERTSCALES*	number of floral scales on a representative spikelet
RACHILLEN*	rachilla length (mm)
SCALEDNSF	number of fertile scales per mm of rachilla: RACHILLEN / FERTSCALES

Table 1. Continued.

Character	Description
SCALEDNSA[R]	floral scale density: SCALENUM / RACHILLEN
SCALERED	reddish intercostal streaking on floral scales (presence/absence)
STRONGRED	deep brick red coloration of floral scales (presence/absence)
SCALELEN[R]	floral scale length (mm) (selected from 2nd thru 4th scale from base of spikelet)
SCALEWID[R]	floral scale half width measured from one margin to keel (mm) (selected from 2nd thru 4th scale from base of spikelet)
SCALERAT	ratio of floral scale length to width: SCALELEN / SCALEWID
SCALEHYMA	width of floral scale hyaline margin (mm)
SCALEWP	distance from floral scale base to widest point (mm)
SCALESHAP	ratio of floral scale distance to widest point to scale length: SCALEWP / SCALELEN
SCALEAP1*	angle of floral scale apex measured using three-point angle
SCALEAP2	angle of floral scale apex measured using four-point angle
MUCROLEN	length of floral scale mucro (mm)
ANTHERLEN*	anther length (mm)
SCALEXS1*	floral scale length minus achene length with style: SCALELEN - ACHENELEN1
SCALEXS2*	floral scale length minus achene length without style: SCALELEN - ACHENELEN2
SCALERAT1*[R]	ratio of achene total length to floral scale length: ACHENELEN1 / SCALELEN
SCALERAT2	ratio of achene body length to floral scale length: ACHENELEN2 / SCALELEN
ACHENELEN1*	achene length including remnant style (mm)
ACHENELEN2[R]	achene body length (not including remnant style) (mm)
ACHENEWMW	achene width at midpoint (mm) (midpoint determine by achene body length)
ACHENEWID[R]	achene width at widest point (mm)
ACHENRAT1*	ratio of achene length to achene width at widest point: ACHENELEN1 / ACHENEWID
ACHENERAT2*	ratio of achene body length to achene width at midpoint: ACHENELEN2 / ACHENEWMW
ACHENWP[R]	distance from achene base to widest point (mm)
ACHENESHP[R]	ratio of distance from achene base to widest point and achene body length: ACHENWP / ACHENELEN2
ACHENEAP[R]	angle of achene apex

The 13 characters employed in the reduced data set were anticpated to be the most useful, based on extensive review of herbarium specimens. Two data matrices were subjected to PCA using the reduced number of variable, one including all OTUs, and another including only *Cyperus cephalanthus* and *C. impolitus*.

Results

Results of PCA of the data set containing the *Cyperus rigens* group (all OTUs) and including 13 morpholigical variables are presented in Table 3 and Figure 10. No clustering based on a priori classification is evident. Variation in principal component one is primarily accounted for by

Table 2. Names of Operational Taxonomic Units (OTUs) included in the morphometric study of the *Cyperus rigens* group using PCA.

OTU name	Number of Observations	Comments
Cyperus cephalanthus	24	This name was applied only to North American specimens.
Cyperus conceptionis Steud.	17	Plants referable to this taxon are from southern Chile. Pedersen (1972) observed that while substantial morphological evidence is diagnoses this species, there is overlap with plants from the east and he therefore included it within *Cyperus rigens* subsp. *rigens*. It was separated for this study due to the 1,000 km disjunction across the Andes Mountains and based on the suspicion that Pedersen may have prematurely dismissed it.
Cyperus impolitus	21	This name was applied only to South American specimens.
Cyperus oostachyus Nees	7	This taxon is represented by smaller plants having ascending rather than spreading spikelets in mid-spike; it is included within *Cyperus rigens* subsp. *rigens* by Pedersen (1972).
Cyperus rigens subsp. *rigens*	44	----------
Cyperus rigens subsp. *rigens* (arenic variant)	3	Plants of this taxon were observed by the author growing in drier sandy soils of a *Butia yatay* (Mart.) Becc. savanna in Argentina and may be worthy of taxonomic recognition; further field and herbarium study is needed.
Cyperus rigens subsp. *serrae*	10	This taxon is conventionally recognized and is distinguished from *C.r.* subsp. *rigens* by smaller and more slender plants with longer floral scales that are strongly brick red in color.
Nonelement	7	These specimens are apparently close relatives to members of the *Cyperus rigens* group but are not referable to any species in the group.

ACHENELEN2, SCALELEN, ACHENWP, SCALEDNSA, and SPIKEDENS. Variation in principal component 2 is mainly due to ACHENEWID, SCALEWID, CULMHT, and ACHENERAT1.

Results of PCA involving just *Cyperus cephalanthus* and *C. impolitus* are presented in Table 4 and Figure 11. Data points of these two taxa overlap, with no indication of morphological distinctness. Principal component 1 is mainly influenced by ACHENEWID, SCALEWID, ACHENELEN2, SCALELEN, and SCABROS, while variation in principal component 2 is due primarily to ACHENESHP, ACHENEWP, and ACHENEAP.

Table 3. Eigenvectors, eigenvalues, and cumulative variance for the first four principal components of PCA of 133 OTUs and 13 morphological variables.

Eigenvectors				
	Prin1	Prin2	Prin3	Prin4
ACHENESHP	-0.128225	0.670085	-0.03688	0.061081
ACHENWP	0.2152	0.534739	0.218977	-0.095023
ACHENEAP	-0.0144	0.304662	-0.428168	0.183048
CULMHT	0.117429	0.152862	0.198364	0.723469
ACHENEWID	0.405719	-0.0337	-0.316595	-0.033989
SCALEWID	0.405619	-0.064485	-0.164455	-0.181503
SCALELEN	0.363073	-0.070086	0.0556	0.202753
SPIKEDENS	-0.280277	-0.072825	-0.153882	0.110213
ACHENRAT1	-0.241569	-0.075583	0.59866	-0.048175
SCABROS	-0.31187	-0.081798	0.023229	0.13556
ACHENELEN2	0.365228	-0.118692	0.286258	-0.151993
ANTHWID	0.2567	-0.175636	0.166384	0.476647
SCALEDNSA	-0.169803	-0.275691	-0.32466	0.26829
Eigenvalues	4.65279053	1.82095839	1.54301219	1.27758425
Cumulative Variance	0.3579	0.498	0.6167	0.7149

Discussion

Graphical PCA results for the *Cyperus rigens* group and comparing *C. cephalanthus* and *C. impolitus* (Figures 10 and 11) provide little resolution regarding which taxa to recognize. The PCA results for the *Cyperus rigens* group are not surprising given how much morphological variation was present in the specimens measured.

There is substantial overlap of data points in the comparison of *Cyperus cephalanthus* and *C. impolitus* (Figure 11), suggesting these two taxa have not morphologically diverged. However, comparison of

some individual characters a significantly different. Table 5 shows results of pair-wise t-tests comparing 13 variables between *Cyperus cephalanthus* and *C. impolitus*. *Cyperus cephalanthus* has wider anthela, longer and wider floral scales, and wider and differently shaped achenes.

Table 4. Eigenvectors, eigenvalues, and cumulative variance for PCA analysis of *Cyperus cephalanthus* and *C. impolitus* using 13 morphological variables.

Eigenvectors				
Variable	Prin1	Prin2	Prin3	Prin4
CULMHT	0.117429	0.152862	0.198364	0.723469
SCABROS	-0.31187	-0.081798	0.023229	0.13556
ANTHWID	0.2567	-0.175636	0.166384	0.476647
SPIKEDENS	-0.280277	-0.072825	-0.153882	0.110213
SCALEDNSA	-0.169803	-0.275691	-0.32466	0.26829
SCALELEN	0.363073	-0.070086	0.0556	0.202753
SCALEWID	0.405619	-0.064485	-0.164455	-0.181503
ACHENELEN2	0.365228	-0.118692	0.286258	-0.151993
ACHENEWID	0.405719	-0.0337	-0.316595	-0.033989
ACHENRAT1	-0.241569	-0.075583	0.59866	-0.048175
ACHENWP	0.2152	0.534739	0.218977	-0.095023
ACHENESHP	-0.128225	0.670085	-0.03688	0.061081
ACHENEAP	-0.0144	0.304662	-0.428168	0.183048
Eigenvalues	4.65279053	1.82095839	1.54301219	1.27758425
Cumulative Variance	0.3579	0.498	0.6167	0.7149

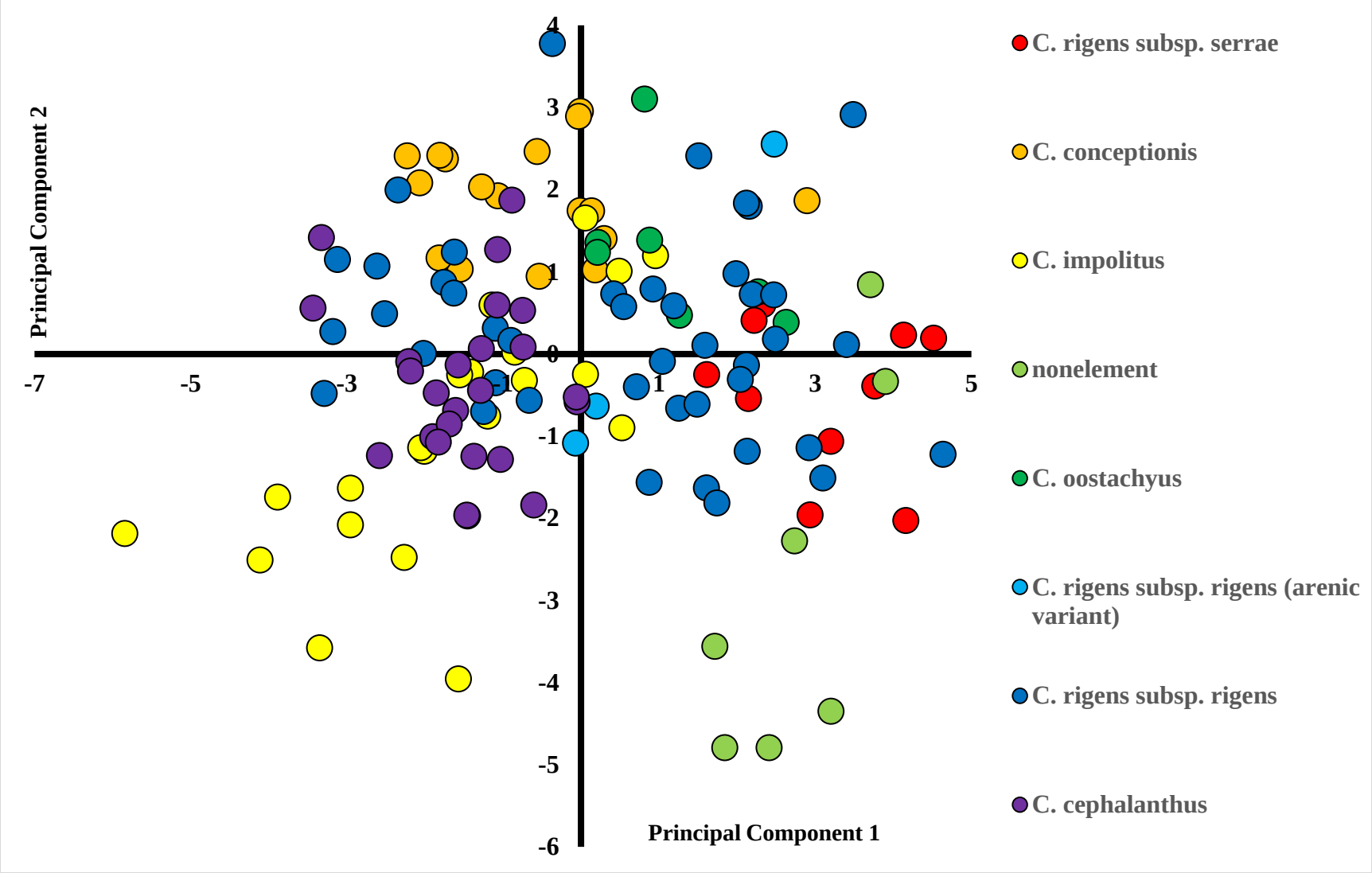

Figure 10. Graphical results of PCA of 133 OTUs representing the *Cyperus rigens* species group using 13 variables.

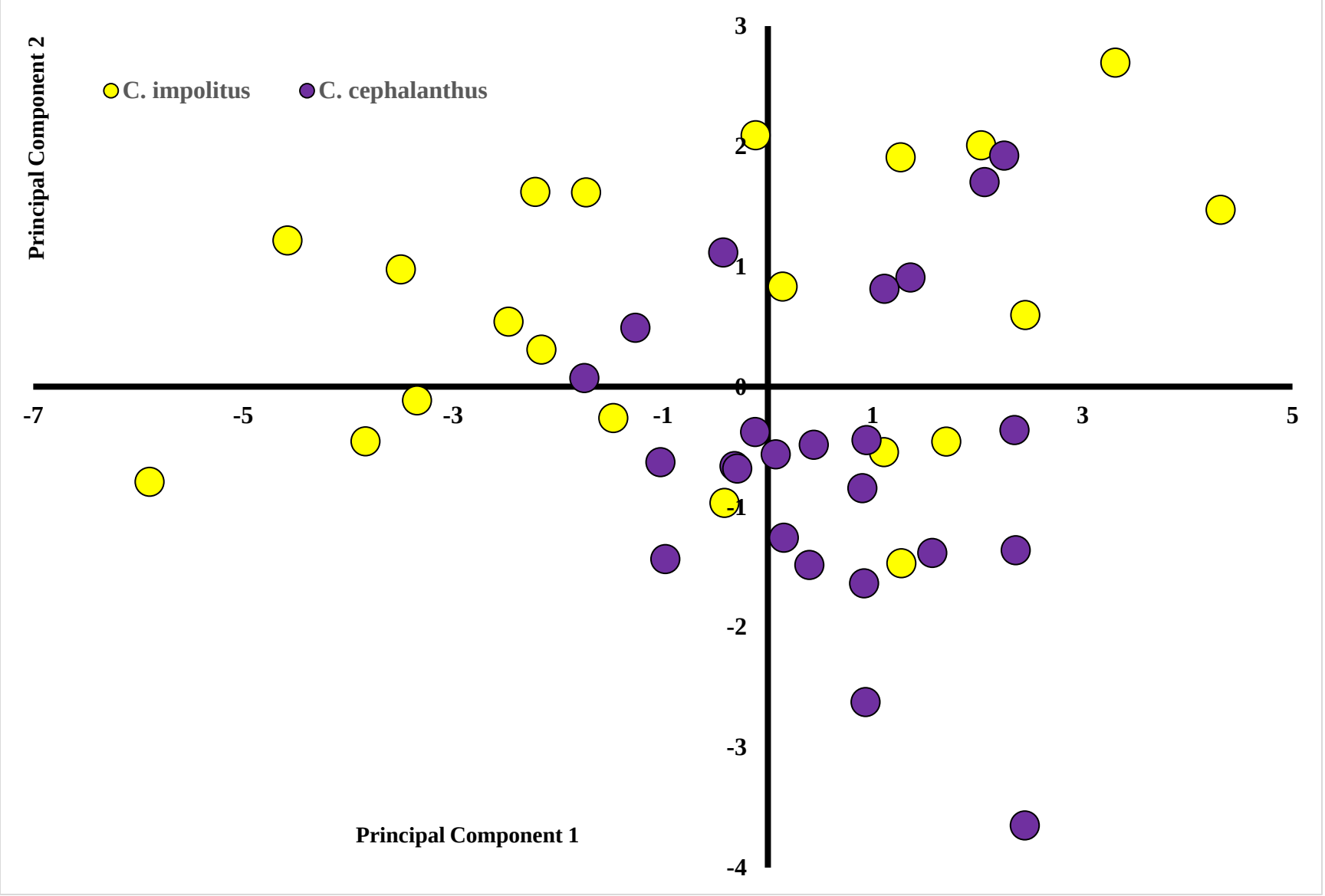

Figure 11. Graphical results of PCA of 45 OTUs representing the *Cyperus cephalanthus* and *C. impolitus* using 13 variables.

Table 5. Comparison of mean values of 13 morphological variables between North American *Cyperus cephalathus* and South American *C. impolitus*, with t-test statistics, and significance indicators (* = significant at alpha = 0.05, ** = significance at alpha = 0.01, NSD = No Significant Difference).

Character	*C. cephalanthus* (n = 24)	C. impolitus (n = 21)	p-value	Significance
CULMHT	110	112.938	0.6812	NSD
SCABROS	18	19.81	0.6079	NSD
ANTHWID	6.0333	4.4119	0.0182	*
SPIKEDENS	52.63	51.71	0.7037	NSD
SCALEDENSA	1.50079	1.43424	0.2452	NSD
SCALELEN	2.86688	2.68314	0.0019	**
SCALEWID	0.65975	0.60929	0.0337	*
ACHENELEN2	1.37854	1.35648	0.4763	NSD
ACHENEWID	0.63521	0.57129	0.0042	**
ACHENWP	0.72721	0.76595	0.0369	*
ACHENESHP	0.52862	0.56581	0.0026	**
ACHENRAT1	2.39071	2.58167	0.0153	*
ACHENAP	87.975	84.8195	0.2569	NSD

Conclusions

This analysis is preliminary, especially regarding the broader *Cyperus rigens* group. Relatively simple statistical analyses show significant differences between *Cyperus cephalanthus* and *C. impolitus* in several morphological variables. This evidence plust the ca 8,000 km disjunction provide ample evidence to uphold these taxa as distinct species. Data collected for this study require more extensive analyses and will be carried out in the near future.

CHAPTER 5.
FLORISTICS OF WET COASTAL PRAIRIES IN SOUTHWEST LOUISIANA

Introduction

The author initially developed an interest in coastal prairie because of the high fidelity of *Cyperus cephalanthus* to this habitat. After initiating the research presented in the previous chapters, the author contributed to the discovery a several important coastal prairie remnants and he has worked to enhance habitat conditions on these sites through the application of prescribed fire. Coastal prairie research and stewardship has been primary focus of the author since 2013 and will remain a priority for the forseeable future.

Coastal prairie is an extension of tall-grass prairie from the eastern Great Plains. This grassland historically occupied 3,600,000 ha in Louisiana and Texas (Smeins et al. 1991). In Louisiana, coastal prairie ranged across a triangular-shaped region from Lafayette to Opelousas to Lake Charles in the southwestern part of the state (Figure 10). Edaphic conditions that retard woody plant growth work in concert with recurring fire to maintain tall-grass prairie in a region otherwise having adequate moisture to support forests (Brown 1972, Allen and Vidrine 1989, Holcomb et al. 2015).

Rangewide, coastal prairie has been reduced to less than one percent of its historical extent by agricultural conversion, incompatible grazing practices, and urban and suburban development (Smeins et al. 1991). Most of Louisiana's prairie has been converted to rice cultivation. Allen and Vidrine (1989) estimated that only 200 ha of intact prairie remain in Louisiana in the form of narrow linear strips along railroad grades. In addition to railroad remnants, there are several wet coastal prairies occurring adjacent to coastal marsh, and at least two urban prairie remnants are known (Grace et al. 2000, Louisiana Natural Heritage Program, unpublished data). Combining all expressions of coastal prairie, well below one percent of the historical extent of coastal prairie remains in Louisiana (Holcomb et al. 2015). While the status of coastal prairie is dire, several additional prairie remnants totaling approximately 1,000 ha have been discovered within the last five years on private ranches in the Lake Charles area (Figure 11). Discovery of these grazed prairies roughly quadrupled the amount of known coastal prairie area in Louisiana.

Allen et al. (2001) provided the most comprehensive report of the vascular flora of Louisiana's coastal prairie by surveying ten railroad remnants scattered across Acadia, Allen, and Jefferson Davis Parishes (Figure 12). Allen et al. (2001) reported 512 species and subspecific taxa from their study sites and determined that 244 of these taxa represented true coastal prairie species, with the balance being characteristic of disturbed areas and inclusional longleaf pine savanna vegetation encountered on northernmost study sites. By comparing their results to those of other parts of North America, Allen et al. (2001) described the flora as being derived primarily from that of the coastal plain and overlain by a Midwestern prairie component.

Coastal prairie in Louisiana occurred at low elevations near the interface with fresh and intermediate marsh inland up to about 16 meters in elevation along the northern edge (Vidrine 2010). Therefore, the

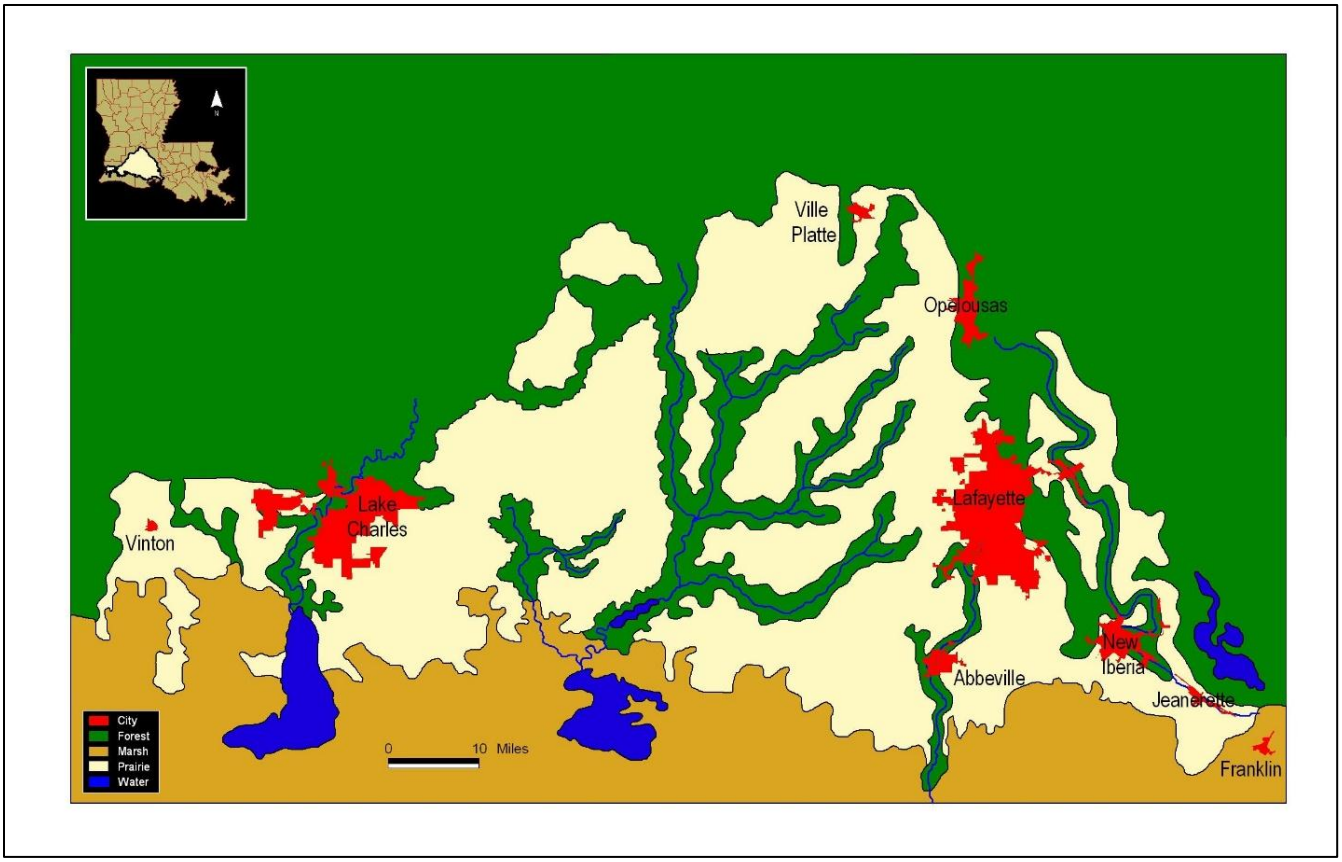

Figure 12. Map showing the historical extent of coastal prairie in southwestern Louisiana. Courtesy of Larry Allain, USGS Wetland and Aquatic Research Center, Lafayette.

prairie was anything but monotonous in terms of vegetation. The study sites of Allen et al. (2001) averaged about 8 m in elevation. Recently discovered coastal prairie remnants, including prairies that are used as rangelands, are closer to the coast and, in some examples, immediately flanking coastal marsh. With the exception of one site, Florence Club Prairie located in Vermilion Parish (Grace et al. 2000), wetter prairies have not been floristically inventoried. Recently discovered grazed coastal prairies, which occur on private ranches, average approximately 150 ha in size and, since they have not been plowed, retain their characteristic considerable areas of broad inter-mound flats (Figure 11). Being narrow strips, railroad prairie remnants do not capture these embedded landscape features, which greatly increase plant species richness by offering additional ecological space. The main motivation to carry out this research was to explore newly discovered prarie remnants to document the flora present and to make field observe on vegetation associations present on the various landsape positions. Included among the study sites are several marsh-fringing coastal prairies supporting *Cyperus cephalanthus*, which was been a recurring interest throughout the author's dissertation research.

Floristic Quality Assessment

Floristic Quality Assessment (FQA) protocols are increasing in popularity as an approach to assess the natural quality of sites. This concept was first developed Swink and Wilhelm (1979) for assessing the quality of remnant plant communities in the Chicago area. With the FQA approach, species in a flora are

Figure 13. The author and Ms. Jenny Kluse from the Shirley C. Tucker Herbarium (LSU) collecting plant specimens from a grazed coastal prairie in May 2015. This site was burned by the author about six weeks prior. Photo by Kyle Harms.

subjectively assigned C-values based on their respective tolerances to disturbance and values as indicators of natural habitat conditions. Swink and Wilhelm (1979) assigned C-values to native species ranging from 0 to 10. Using C-values, a Floristic Quality Index (FQI) can be calculated for a given site by the following formula:

$$\mathrm{FQI} = \mathrm{C}\sqrt{\mathrm{n1}}$$

Where C is the average coefficient of conservatism and $\sqrt{\mathrm{n1}}$ is the square root of the number of native species at the site (Swink and Wilhelm 1979). This formula ignores exotic species, which do not receive C-values. Allain et al. (2004) presented a FQA for Louisiana Coastal Prairie based on the flora reported from railroad prairies by Allen et al. (2001). The FQI of Allain et al. incorporates exotic species, presenting an adjusted FQI:

$$\mathrm{AFQI} = \mathrm{C}\sqrt{\mathrm{n2}}$$

Where $\sqrt{n2}$ is the square root of all species occurring at a site. In the FQA of Allain et al. (2004), C-values ranged from -3 to 10, with exotic species receiving negative integers. While the general purpose is constant, C-value assigments and FQI formulas vary slightly across various FQA systems. For example, Cretini et al. (2012) assigned a value of 0 to nonnative species, and values ranging from 1 to 10 for natives for their FQA of coastal marshes in Louisiana. The FQI formula of Cretini et al. (2012) incorporates abundance data (rather than presence/absence) and scales the FQI score from 0 to 100.

An additional goal of this work was to assign coefficients of conservatism (C-values) to each species documented in the wet coastal prairie flora. The FQA protocol described here differs slighty from that of Allain et al. (2004), which was based on a checklist from railroad remnants. This is because the sites represented in the present study are wetter and most of them are currently grazed by cows. Grazing is a disturbance source not found on railroad remnants and has the effect of causing shifts in species' abundances based on grazing preferences (Grelen and Duvall 1966).

The C-values assigned as part of this research will allow assessments of floristic quality of individual sites in the region, ranging from prairie remnants to *de novo* restorations. A timely application of FQA of wet coastal prairie is assessing restoration progress on wetland mitigation banks, which have recently increased in frequency in the focal area of this study.

Materials and Methods

Specimen collection for this study was focused on five sites: Coulee Jack, Cox, Deer Ridge, Gray, and Gum Cove Prairies. Deer Ridge Prairie is located on White Lake Wetlands Conservation Area in Vermilion Parish and is the only coastal prairie remnant occurring on a publicly-owned conservation area. The remaining primary study sites are grazed prairies occurring on private ranches in Calcasieu and Cameron Parishes. The flora also includes taxa reported from Florence Club Prairie (Grace et al. 2000) and collections from occasional visits to several sites including a railroad prairie near Vinton (very near Gray Prairie) in Calcasieu Parish, a small urban remnant in Carlyss (vicinity of Lake Charles/Sulphur), and two prairie remnants south of Lake Charles just into Cameron Parish that are captured by wetland mitigation banks. The nine study sites are located further west and in closer proximity to the coast compared to study sites of Allen et al. (2001) (Figure 12). Data for this flora was also obtained from specimens deposited at the Shirley C. Tucker Herbarium (LSU) collected from wet prairies in Calcasieu and Cameron Parish.

In the checklist resulting from this work, scientific names follow USDA, NRCS (2015) in most cases. In cases of revised taxonomy, alternative scientific names are used. Family assignments follow USDA, NRCS (2015). Difficult specimens were sent to specialists for verification, when assistance was needed (e.g. *Dichanthelium*). Wetland indicator status for each taxon was determined by consulting Lichvar et al. (2016). Infraspecific taxa are not assigned wetland indicator statuses.

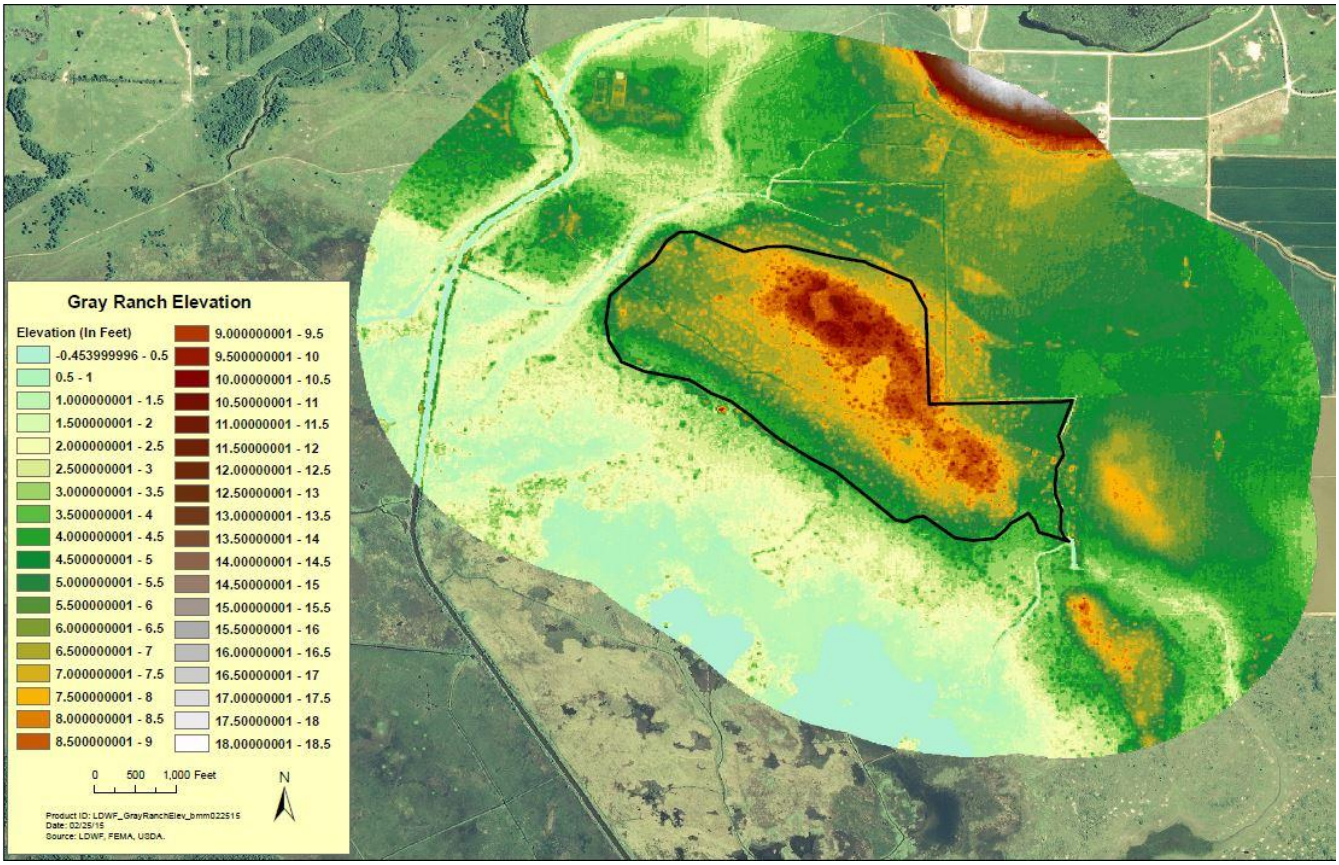

Figure 14. LiDAR (Light Detection and Ranging) imagery for Gray Prairie in Calcasieu Parish showing micro-topographic variation resulting from numerous pimple mounds and several isolated ephemeral ponds. The intermediate marsh which is symbolized by yellow, yellow-green, and light blue colors and occurs southwest of the black polygon which captures most of the coastal prairie.

Once the list of species was complied from on fieldwork and herbarium study, C-values were assigned by a working group consisting of the author, Dr. Lowell Urbatasch, and Mr. Larry Allain. These three botanists possessed adequate expertise with the regional flora. For this exercise, C-values ranged from -3 to 10. Table 6 presents criteria used in C-vlaue assignment. A combination of disturbance tolerance and prairie indicator value were considered. Invasive species were eligible for C-values of 0 to -3, with the lower numbered taxa being more invasive. The lowest C-value assigned to native species was 1, which was applied to the weediest taxa.

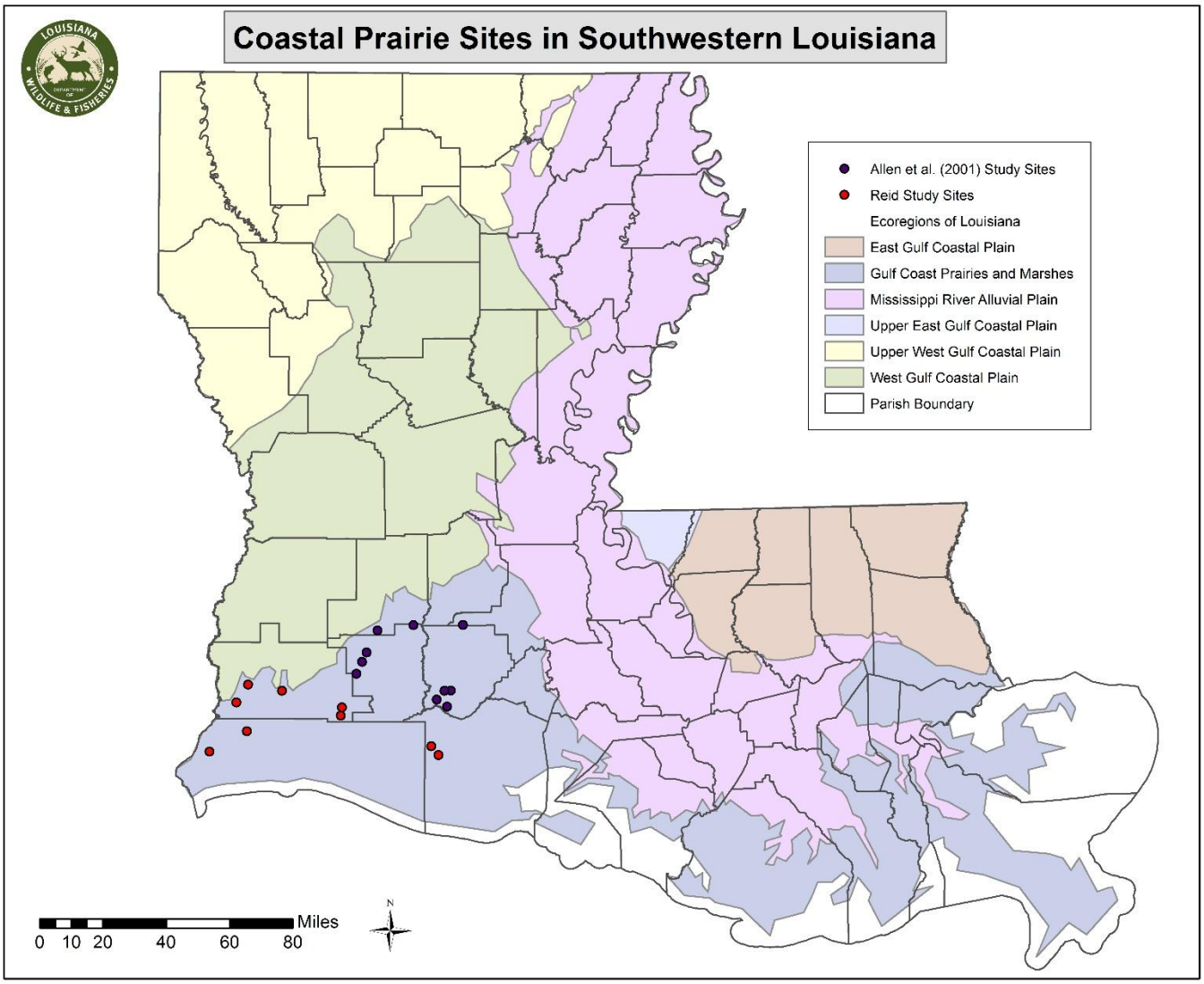

Figure 15. Locations of sites explored for this project and study sites of Allen et al. (2001).

Results

In this first approximation, 512 species and subspecific taxa were documented in the wet coastal prairie flora. This is the same number of taxa as reported for railroad remnants further inland (Allen et al. 2001). The documentation of the same number of taxa between the two prairie floras is due to chance and means nothing, as both surveys were preliminary in nature. The flora of wet coastal prairies is presented in Appendix 4. Annotations for each species include C-value, wetland indicator status, and voucher specimen. There were 51 species of nonnative plants in the flora, amounting to ~10 % of the flora. Fifteen taxa appear on the list on the basis of older specimens and were not collected or observed for this study; therefore, these taxa are regarded as historical until they are confirmed to be extant. Most of the historical taxa are highly conservative. *Andropogon gerardii* is a superb forage grass (Grelen and Duvall (1966) and the failure to document it in the present study may be due to past grazing pressure.

Table 6. Criteria for C-value assignment to members of the wet prairie flora in southwest Louisiana.

C-Value Classes	Criteria
-3 - 0	Nonnative species; taxa assigned C-value of 0 are innocuous exotics. Negative numbers are assigned based on degree of invasiveness, with -3 being reserved for the most aggressive taxa.
1 - 3	Taxa in this class are site generalists, including mostly early successional species; these taxa have no value in predicting the presence of coastal prairie habitat. In addion to early successional taxa, those taxa characteristic of non-prairie habitats often fall into this class. For example, those taxa typical of forests that become established on a coastal prairie remnant in the absence of fire.
4 - 6	Taxa receiving C-values in this range include coastal prairie species to cal tolerate moderate to heavy site perturbation from soil disturbance or heavy grazing; these taxa tend to be more frequent across a disturbed landscape and have dispersal abilities allowing them to colonize previously plowed land. Taxa making it into this C-value range are those thought to have been components of the coastal prairie in pristine times.
7 - 8	These taxa are conservative coastal prairie taxa that tolerate mild disturbance and have high coastal prairie predictive value.
9 - 10	Taxa in this range are not disturbance tolerant and whose presence indicates the occurrence of coastal prairie with practically 100% accuracy.

A total of 82 families were represented, the most species rich being Poaceae (102 taxa), Cyperaceae (72 taxa), and Asteraceae (67 taxa). The two largest genera were *Cyperus* (20 taxa) and *Rhynchospora* (18 taxa), both members of Cyperaceae. The grass genera *Dichanthelium* and *Paspalum* followed in species richeness with 12 and 14 taxa, respectively.

Of the 461 native taxa documented, 255 are thought to be characteristic of the prairie. This number is computed by summing the number of taxa with C-values of 4 or higher (Figure 13). Some taxa having lower C-values may have been present historically on highly disturbed sites. The 206 native taxa are characteristic of disturbed areas or are typical of adjacent habitats such as coastal marsh and bottomland hardwood forests. Offsite plants have become established on coastal prairie probably in large part to altered fire regimes. Both AFQI and FQI were calculated for several study site (Table 8).

264 of the 461 (57%) native taxa were also reported by Allen et al. (2001) from railroad prairies. Of the 255 wet prairie species with C-values of 4 or higher, 161 (63%) were also documted from railroad remnants (Allen et al. 2001). Taxa having wetland indicator statuses of OBL, FACW, and FAC are regarded as hydrophytes (Lichvar et al. 2016). Of the 512 taxa documented, 342 taxa (~ 67%) are hydrophytes (Figure 14). Nonhydrophytes occurred mainly on pimple mounds.

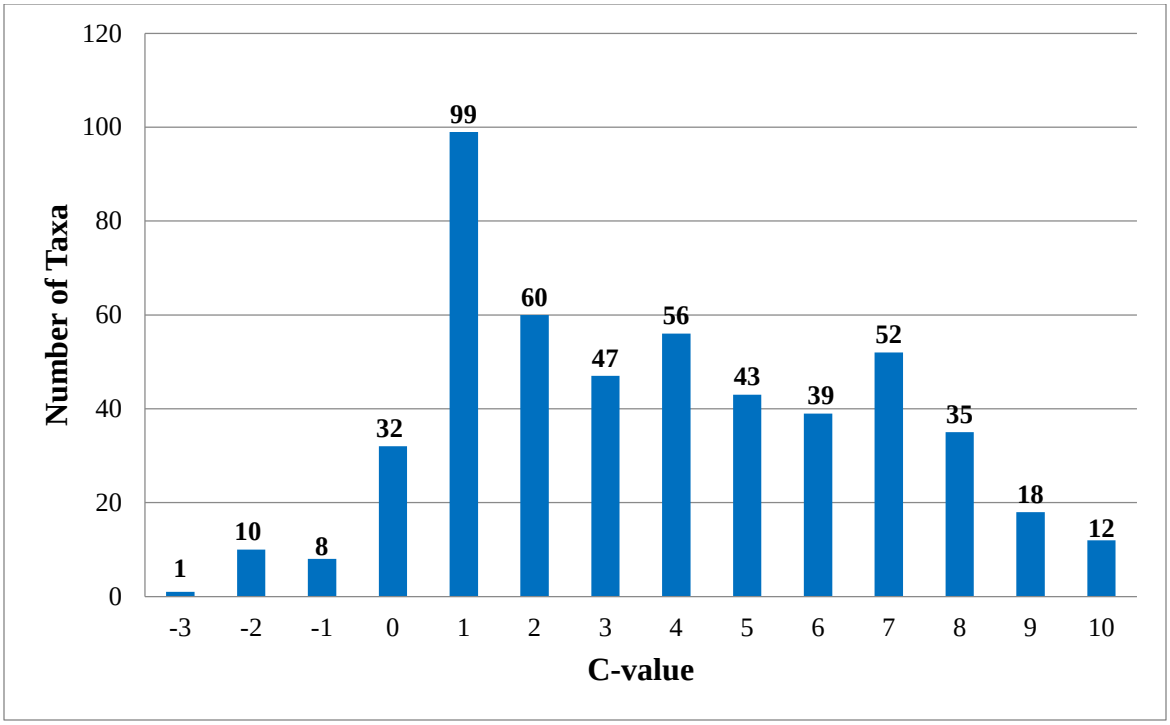

Figure 16. Number of taxa for each coefficient of conservatism (C-value).

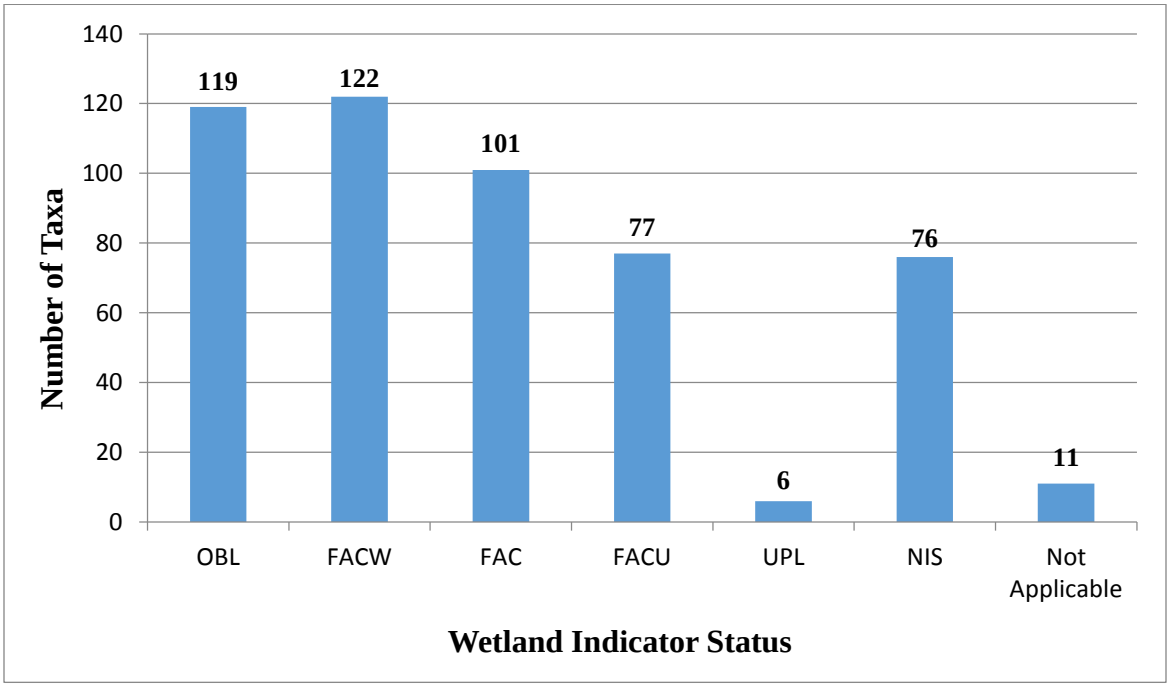

Figure 17. Number of taxa for wetland indicator status. “Not Applicable” captures infrascpeific taxa whose wetland status differs from the nominal variety based on field observations during this study. Species whose status is “NIS” have no wetland indator status and therefore are assumed to not occur in wetlands anywhere in their range.

Table 7. Plants characteristic of the different landscape positions support on wet coastal prairies in southwestern Louisiana.

Inter-mound Flats (broad-scale, hydric to occasionally mesic)		
Amsonia rigida	*Hypericum densiflorum*	*Rhynchospora elliottii*
Arnoglossum ovatum	*Hibiscus leucophyllus*	*Rhynchospora glomerata*
Asclepias longifolia subsp. *hirtella*	*Iva angustifolia*	*Rhynchospora inexpansa*
Axonopus fissifolius	*Juncus biflorus*	*Rhynchospora rariflora*
Carex complanata	*Juncus brachycarpus*	*Rosa bracteata*
Carex meadii	*Juncus dichotomus*	*Rudbeckia texana*
Carex microdonta	*Limnosciadium pumilum*	*Ruellia humilis*
Centella erecta	*Lobelia puberula*	*Sabatia campestris*
Dichanthelium scoparium	*Paspalum plicatululum*	*Schizachyrium scoparium*
Eleocharis montevidensis	*Pycnanthemum tenuifolium*	*Sporobolus indicus*
Eupatorium hyssopoifolium	*Rhexia mariana*	*Tridens strictus*
Fimbristylis puberula	*Rhynchospora caduca*	
Marsh-fringing Inter-mound Flats (broad-scale, hydric) (* denotes species occurring in prairie flanking strictly freshwater marsh)		
Andropogon glomeratus	*Dichanthelium oligosanthes* subsp. *oligosanthes*	*Paspalum praecox* *Rhynchospora colorata*
Boltonia asteroides	*Fimbristylis caroliniana*	*Rhynchospora elliottii*
**Carex verrucosa*	*Helenium flexuosum*	*Rhynchospora globularis* var. *pinetorum*
**Cladium mariscus subsp. jamaicense*	*Hibiscus leucophyllus*	*Rhynchospora perplexa*
Coreopsis tinctoria	*Iva angustifolia*	*Spartina patens*
**Cyperus cephalanthus*	*Lythrum alatum* var. *lanceolatum*	
**Cyperus reflexus* var. *fraternus*	*Panicum virgatum*	
Dichanthelium dichotomum var. *nitidum*	*Paspalum plicatulum*	
Pimple Mounds (small-scale, mesic to subxeric)		
Andropogon ternarius	*Hymenopappus artemisiifolius*	*Sassafras albidum*
Andropogon virginicus	*Ilex vomitoria*	*Schizachryium scoparium*
Asclepias obovata	*Lobelia appendiculata*	*Schizachyrium tenerum*
Chrysopsis pilosa	*Mimosa hystricina*	*Scleria pauciflora* var. *pauciflora*
Croton michauxii var. *ellipticus*	*Monarda punctate*	*Scutellaria integrifolia*
Cyperus retrorsus	*Paspalum notatum*	*Scutellaria parvula*
Dichanthelium aciculare	*Paspalum setaceum*	*Solidago rugose*
Dichanthelium filiramum	*Rhynchospora globularis* var. *globularis*	*Stillingia sylvatica*
Eupatorium capillifolium	*Rhynchospora recognita*	*Tradescantia hirsutiflora*
Helianthus mollis	*Salvia azurea*	

Table 7 (continued).

Ephemeral Ponds (small-scale, hydric)		
Bacopa caroliniana	*Panicum hemitomon*	*Rhynchospora glomerata*
Eleocharis quadrangulata	*Paspalum modestum*	*Rhynchospora macrostachya*
Gratiola brevifolia	*Paspalum praecox*	*Rhynchospora perplexa*
Juncus nodatus	*Pontederia cordata*	*Xyris difformis* var. *difformis*
Leersia hexandra	*Proserpinaca palustris*	*Xyris laxifolia* var. *iridifolia*
Myriophyllum pinnatum	*Proserpinaca pectinata*	
Alkali/Sodic Slicks (small-scale, hydric)		
Bacopa monnieri	*Heliotropium curassavicum*	*Spergularia salina*
Cynodon dactylon	*Houstonia rosea*	*Sporobolus pyramidatus*
Eustoma exaltata	*Samolus ebracteatus*	
Fimbristylis castanea	*Spartina spartinae*	

Rangeland prairie such as Gray, Coulee Jack, Cox, and Gum Cove featured considerable micro-tographic variation. Most area within study sites was occupied by hydric broad flats (sometimes approaching mesic). Pimple mounds, which are small circular soil mound thought to be of aeolian origin (Seifert et al. 2009) were abundant on several sites. Two prairies situated near the interface of intermediate marsh featured alkali or saline "slicks", possibly formed by salts being concentrated due to the wicking action of pimple mound soils (Andrew Sipocz, personal communication). Characteristic plant species of these various landscape positions are listed in Table 7.

Several species at the state or regional level were documented from study sites: *Carex microdonta*, *C. meadii*, *Cyperus cephalanthus*, *Euphorbia bicolor*, *Ludwigia microcarpa*, *Rudbeckia texana*, *Samolus ebracteatus*, and *Scleria verticillata*. The second known Louisiana collection of the diminutitive sedge *Cyperus hemidrummondii*, a predominantly western species, was made (Sorrie and LeBlond 2008). Several species were documented in Louisiana for the first time. The natural ranges of *Eragrostis silveana* and *Isolepis cernua* were expanded slightly eastward from adjacent Texas (Smith 2002, Peterson 2003). The exotic *Paspalum scrobiculatum* was documented at one site; this Old World species was known only from Texas in the United States (Allen and Hall 2003). A collection of a distinctive grass proved to be *Chrysopogon pauciflorus* (Figure 17). The primary range of this species is peninsular Florida and Cuba, with at least one record from Jefferson County, Texas, which borders Calasieu Parish (Hall and Thieret 2003). *Chrysopogon pauciflorus* was abundant at one coastal prairie remnant in the fall following a spring burn, but was not observed during a non-burn year.

Table 8. AFQI and FQI scores for four wet prairie remnants surveyed for this study.

Prairie Name	Approx. Size (ha)	Survey Intensity	# Total Species	Avg. C-Value	AFQI	# Native Species	Avg. C-Value (natives)	FQI
Gray	360	High	331	3.67	66.73	304	4.07	70.95
Gum Cove	45	High	256	3.22	51.56	224	3.80	56.86
Coulee Jack	200	Moderate	202	4.00	56.92	186	4.45	60.67
Cox	300	Low	137	4.76	55.70	132	5.05	57.97

Figure 18. Specimen of *Chrysopogon pauciflorus* collected from a wet coastal prairie in southwestern Louisiana. This specimen represents the first record of this species from Louisiana.

Discussion

The wet prairie flora has a strong wetland component with upland species mostly occurring on pimple mounds. Obtaining a picture of what the coastal prairie flora was like historically is made impossible by the fact that so little prairie remains, and remnants are invariably degraded by altered fire regimes, soil disturbance, aerial herbicide application, and historical episodes of heavy grazing. These factors introduce ecological "noise". The flora of most of the study sites consisted of mixes of characteristic prairie elements, early successional indicators of disturbance, plants that increase under grazing, and substantial amounts of woody encroachment. Deer Ridge Prairie, which occurs on an "island" embedded in freshwater marsh, has a wet prairie component plus species expanding from the adjacent marsh.

Portions of Gray and Gum Cove Prairies, which located at the terminus of the Prairie Terrace, support zones referable to Marsh-Fringing Coastal Prairie, an ecological association (CEGL007936) recognized in the National Vegetation Classification (NVC) (USNVC 2016). This ecological association concept is based on coastal prairie examples at Florence Clube and Deer Ridge, sites included in this flora. On the more mesic end, small portions of Coulee Jack Prairie support inter-mound flats dominated by *Schizachyrium scoparium*; this dominant grass plus other elements such as *Panicum virgatum* and *Sorghastrum nutans* would result in classification of this area as Eastern Upland Coastal Prairie (CEGL007938) (USNVC 2016). Eastern Upland Coastal Prairie has the greatest resemblance to Midwestern tall-grass prairie that any other expression of coastal prairie in Louisiana. While portions of sites do answer to existing ecological associations, most of the area captured by the study sites defies classification. There are two possible reasons for this: 1) most of the wet prairies studied represent coastal prairie types that are not accounted for in existing vegetation classification systems; and 2) ecological noise present on many sites obscures the natural state of these prairies.

Observations from this study suggest that perhaps both possibilities are at least partly true. While *Schizachyrium scoparium* and *Paspalum plicatulum* are both characteristic coastal prairie species, the former decreases with grazing pressure while the latter increases. *Paspalum plicatulum* is co-dominant in hydric inter-mound flats at one grazed prairie surveyed for this study. At this site, Schizachyrium scoparium is present but uncommon on inter-mound areas and is locally abundant on some pimple mounds. Since cows differentially use pimple mounds, and considering that *Schizachyrium scoparium* offers preferred forage, the expectation would be for S. scoparium to have been elimated or nearly so from pimple mounds. This observation suggests a preference by *Schizachyrium scoparium* of drier sites. The interaction between abiotic site variables and grazing is a topic in need of study. The author currenty has employed a series of cattle exclosures aimed at gaining more information on prairie maintainance as affected by cattle grazing.

Conclusions

This study presents a preliminary survey of the vascular flora of wet coastal prairie remnants in close proximity to the interface with coastal marsh. A total of 512 vascular plants, including 461 native taxa and 255 prairie taxa were documented. Several notworthy discoveries were made, including popualtions of regionally rare species, and documentation of four species in Louisiana for the first time. Finer scale research relating vegetation to site variables and grazing are underway by the author.

CONCLUSIONS

The content of this research was diverse, including molecular systematics, morphology-based studies, and with a field botany element. Phylogenetic studies of *Cyperus* yielded some important information. The phylogenetic position of the monotypic genus *Karinia* was estimated for the first time. Molecular and morphological evidence support inclusion of this genus within *Scirpoides*. Mesoamerican taxa *Cyperus andinus* and *C. seslerioides* are related to *C. schomburgkianus*, a member of section *Leucocephali*. Section *Leucocephali* is resolved as sister to C_4 *Cyperus*. This finding is significant since members of section *Leucocephali* are adapted to seasonally dry, often rocky grasslands, and may represent a critical precursor to the evolution of C_4 photosynthesis. This innotation apparently allowed colonization of various seasonally dry to xeric habitats not previously accessible to *Cyperus*. Additional support of the monophyly of the American section *Luzuloidei* was gained. Section *Diclidium* was shown to be polyphyletic and thus artificial. These and other smaller insights contribute to the efforts of botanists across the globe to learn more about this massive plant group. A "complete" phylogenetic hypothesis for *Cyperus* will require a large collaborative effort. The author is a now part of the global sedge community and anticipates continuing his phylogenetic work with this group.

Morphological studies within the *Cyperus rigens* group showed that *Cyperus cephalanthus* and *C. impolitus* are morphologically the same species. These taxa exhibit an amphitropical disjunction. Morphometric results are consistent with one or few long distance dispersal events giving rise to North American populations of *Cyperus cephalanthus*/*impolitus*. Only a small range of the morphological variation present in South American populations is found in North American populations.

Interest in *Cyperus cephalanthus* motivated some field trips by the author to coastal prairie remnants early on. However, the discovery of some very promising prairie remnants ignited the author's interest for this rare grassland. The wetter expression of coastal prairie has been botanically neglected. The floristic analysis of wet coastal prairie resulted in documentation of 512 taxa with strong representation by hydric plants. Four species not previsouly reported from Lousiana were discovered. Coefficients of conservatism were assigned to each taxon to enable calculation of Floristic Quality Indices for prairie remnants and re-establishment sites in the future.

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APPENDICES

APPENDIX 1:
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Affiliation: Louisiana State University, Biological Sciences

Street: 202 Life Sciences Bldg.

Street:

City: Baton Rouge

State: LA

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Full name(s) of author(s): Christopher S. Reid

Publisher: Louisiana State University

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Proposed publication date: December 2016

Format(s) of publication (e.g., paperback, hardcover, website, interpretive signage): PhD Dissertation chapter

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Appendix 1 (continued)

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Boom, Brian <BBoom@nybg.org>

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Thanks for publishing these research results in Brittonia, and best of success with your dissertation!

Sincerely,

Brian Boom

Brian M. Boom, Ph.D.
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Director, NYBG Press and Science Outreach
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APPENDIX 3.
TAXA INCLUDED IN PHYLOGENETIC ANAYLSIS OF NUCLEAR ITS SEQUENCES (CHAPTER 2) WITH COLLECTION LOCALITIES, VOUCHER SPECIMEN INFORMATION, AND GENBANK ACCESSION NUMBERS.

Taxon	Collection Locality	Voucher Specimen	GenBank Accession No.
Bulbostylis densa (Wall.) Hand.-Mazz.	----------	----------	AB261663.1
Carex decomposita Muhl.	----------	----------	AY757411.1
Kyllinga sp.	Dade County, Florida	Carter 18739 (VSC)	KF146651
Cyperus acuminatus Torr. & Hook.	Sabine Parish, Louisiana	Reid 6171 (LSU)	KF146652
Cyperus aggregatus (Willd.) Endl. (Louisiana)	Allen Parish, Louisiana	Reid 7620 (LSU)	KF146653
Cyperus aggregatus (Willd.) Endl. (Argentina)	Corrientes, Argentina	Reid 7806 (LSU)	KF193566
Cyperus amuricus Maxim.	----------	----------	JX644852.1
Cyperus articulatus L.	Plaquemines Parish, Louisiana	Reid 7487 (LSU)	KF150538
Cyperus cayennensis Willd. ex Link	Corrientes, Argentina	Reid 7815 (LSU)	KF150539
Cyperus cephalanthus Torr. & Hook. (Louisiana)	Vermilion Parish, Louisiana	Reid 7058 (LSU)	KF150540
Cyperus cephalanthus Torr. & Hook. (Texas)	Brazoria Co., Texas	Reid and Rosen 7510 (LSU)	KF193567
Cyperus compressus L. (Georgia)	Lowndes Co., Georgia	Reid and Carter 7761	KF193575
Cyperus compressus L. (Louisiana)	St. Charles Parish, Louisiana	Reid 7580 (LSU)	KF150541
Cyperus corymbosus Rottb.	Corrientes, Argentina	Reid 7878 (LSU)	KF150542
Cyperus croceus Vahl	Tangipahoa Parish, Louisiana	Reid 7501 (LSU)	KF150543
Cyperus cuspidatus Kunth	Lowndes County, Georgia	Reid and Carter 7760 (LSU)	KF150544
Cyperus cyperoides (L.) Kuntze	----------	----------	AB261665.1
Cyperus dichrostachyus Hochst. ex A. Rich.	----------	----------	JX566744.1
Cyperus difformis L.	St. Charles Parish, Louisiana	Reid 7579 (LSU)	KF150545
Cyperus digitatus Roxb.	Chambers County, Texas	Reid and Rosen 7505 (LSU)	KF150546
Cyperus distinctus Steud.	Camden County, Georgia	Reid and Carter 7744 (LSU)	KF150547

Appendix 3 (continued)

Appendix 3 (continued)

Taxon	Collection Locality	Voucher Specimen	GenBank Accession No.
Cyperus echinatus (L.) Alph. Wood (typical)	Cherokee County, Georgia	Reid and Carter 8044 (LSU)	KF150548
Cyperus echinatus (L.) Alph. Wood ("var. *sphaericus*")	Tangipahoa Parish, Louisiana	Reid 7504 (LSU)	KF150549
Cyperus elegans L.	St. Tammany Parish, Louisiana	Reid 7722 (LSU)	KF150550
Cyperus eragrostis Lam.	Harris County, Texas	Reid 7514 (LSU)	KF150551
Cyperus erythrorhizos Muhl. (north Louisiana)	Morehouse Parish, Louisiana	Reid 7530 (LSU)	KF193571
Cyperus erythrorhizos Muhl. (south Louisiana)	St. Charles Parish, Louisiana	Reid 7578 (LSU)	KF150552
Cyperus esculentus L. var. leptostachyus Boeck.	Plaquemines Parish, Louisiana	Reid 7481 (LSU)	KF150553
Cyperus esculentus var. *macrostachyus* Boeck.	Plaquemines Parish, Louisiana	Reid 7630 (LSU)	KF193572
Cyperus filiculmis Vahl	Beauregard Parish, Louisiana	Reid 7627 (LSU)	KF150554
Cyperus flaccidus R. Br.	----------	----------	JX644855.1
Cyperus fuscus L.	St. Charles Parish, Louisiana	Reid 7788 (LSU)	KF150555
Cyperus grayoides Mohlenbr.	Bienville Parish, Louisiana	Reid 7703 (LSU)	KF150556
Cyperus haspan L.	Allen Parish, Louisiana	Reid 7525 (LSU)	KF150557
Cyperus hystricinus Fernald (north Louisiana)	Bienville Parish, Louisiana	Reid 7705 (LSU)	KF193573
Cyperus hystricinus Fernald (south Louisiana)	Allen Parish, Louisiana	Reid 7520 (LSU)	KF150558
Cyperus imbricatus Retz.	Corrientes, Argentina	Reid 7807 (LSU)	KF150559
Cyperus insularis Heenan & de Lange	New Zealand	----------	DQ385560.1
Cyperus iria L.	Corrientes, Argentina	Reid 7799 (LSU)	KF150560
Cyperus isocladus Kunth	Florida	Abbott 24946 (FLAS)	KF150561
Cyperus lancastriensis Porter	Dawson County, Georgia	Reid and Carter 8043 (LSU)	JX661627.1
Cyperus lecontei Torr. ex Steud.	Florida	Abbott 23732 (FLAS)	KF150562
Cyperus ligularis L.	Florida	Abbott 23681 (FLAS)	KF150563
Cyperus lupulinus (Spreng.) Marcks	Bienville Parish, Louisiana	Reid 7711 (LSU)	KF150654

Appendix 3 (continued).

Taxon	Collection Locality	Voucher Specimen	GenBank Accession No.
Cyperus luzulae (L.) Rottb. ex Retz.	Corrientes, Argentina	Reid 7808 (LSU)	KF150565
Cyperus macrocephalus Liebm.	Tamaulipas, Mexico	Reid 7161 (LSU)	KF150566
Cyperus microiria Steud.	----------	----------	JX644858.1
Cyperus nipponicus Franch. & Sav.	----------	----------	JX644859.1
Cyperus ochraceus Vahl	Brazoria County, Texas	Reid and Rosen 7512 (LSU)	KF150567
Cyperus odoratus L. (Argentina)	Corrientes, Argentina	Reid 7798 (LSU)	KF150568
Cyperus odoratus L. (Louisiana)	Cameron Parish, Louisiana	Reid 7266 (LSU)	KF150569
Cyperus orthostachyus Franch. & Sav.	----------	----------	JX644860.1
Cyperus ovatus Baldw.	Hamilton County, Florida	Reid and Carter 7765 (LSU)	KF150570
Cyperus oxylepis Nees ex Steud.	Plaquemines Parish, Louisiana	Reid 7476 (LSU)	KF150571
Cyperus pacificus (Ohwi) Owhi	----------	----------	JX644861.1
Cyperus papyrus L.	----------	----------	AY242048.1
Cyperus pilosus Vahl	Tangipahoa Parish, Louisiana	Reid 7575 (LSU)	KF150572
Cyperus planifolius Rich.	Dade County, Florida	Mears 5495 (LSU)	KF150573
Cyperus plukenetii Fernald	Taylor County, Georgia	Reid and Carter 8039 (LSU)	KF150574
Cyperus prolifer Lam.	Florida	Abbott 25162 (FLAS)	KF150575
Cyperus prolixus Kunth	Corrientes, Argentina	Reid 7902 (LSU)	KF150576
Cyperus pseudovegetus Steud.	Lanier County, Georgia	Reid and Carter 8035 (LSU)	KF150577
Cyperus pulchellus R. Br.	----------	----------	JX566736.1
Cyperus reflexus Vahl	Corrientes, Argentina	Reid 7869 (LSU)	KF150578
Cyperus retroflexus Buckley	Bienville Parish, Louisiana	Reid 7707 (LSU)	KF150579
Cyperus retrorsus Chapm. (North Carolina)	Buncombe County, North Carolina	Carter 19850 (VSC)	KF150580
Cyperus retrorsus (south Louisiana)	Tangipahoa Parish, Louisiana	Reid 7502 (LSU)	KF193569
Cyperus retrorsus (north Louisiana)	De Soto Parish, Louisiana	Reid 6144 (LSU)	KF193570

Appendix 3 (continued).

Taxon	Collection Locality	Voucher Specimen	GenBank Accession No.
Cyperus rigens J. Presl & C. Presl	Corrientes, Argentina	Reid 7885 (LSU)	KF150581
Cyperus rigens subsp. *serrae* (Boeck.) Pedersen	Corrientes, Argentina	Reid 7868 (LSU)	KF193568
Cyperus rotundus L.	Florida	Abbott 23635 (FLAS)	KF150582
Cyperus spiralis Larridon	Africa	Wingfield 497 (K)	JX566740.1
Cyperus squarrosus L.	Plaquemines Parish, Louisiana	Reid 7554 (LSU)	KF150583
Cyperus strigosus L. (Louisiana)	St. Charles Parish, Louisiana	Reid 7581 (LSU)	KF150584
Cyperus strigosus (Texas)	Chambers County, Texas	Reid and Rosen 7508 (LSU)	KF193574
Cyperus surinamensis Rottb.	Plaquemines Parish, Louisiana	Reid 7478A (LSU)	KF150585
Cyperus tenuispica Steud.	----------	----------	JX644863.1
Cyperus tetragonus Elliott	Glynn County, Georgia	Reid and Carter 7752 (LSU)	KF150586
Cyperus thyrsiflorus Jungh.	Brazoria County, Texas	Reid and Rosen 7511 (LSU)	KF150587
Cyperus ustulatus A. Rich.	New Zealand	----------	DQ385561.1
Eleocharis tuberculosa (Michx.) Roem. & Schult.	----------	----------	FJ826559.1
Ficinia nodosa (Rottb.) Goetgh., Muasya, & D.A. Simpson	----------	----------	DQ385568.1
Fimbristylis autumnalis (L.) Roem. & Schult.	----------	----------	AB250627.1
Fuirena robusta Kunth	Corrientes, Argentina	Reid 7814 (LSU)	KF150588
Hypolytrum nemorum (Vahl) Spreng.	----------	----------	AY242046.1
Isolepis carinata Hook. & Arn. ex Torr.	Catahoula Parish, Louisiana	Reid 7962 (LSU)	KF150589
Juncus effusus L.	----------	----------	AY727793
Kyllinga brevifolia Rottb.	Glynn County, Georgia	Reid and Carter 7755 (LSU)	KF150590
Kyllinga odorata Vahl	Glynn County, Georgia	Reid and Carter 7753 (LSU)	KF150591
Kyllinga pumila Michx.	Glynn County, Georgia	Reid and Carter 7754 (LSU)	KF150592
Lipocarpha humboldtiana Nees	Corrientes, Argentina	Reid 7852 (LSU)	KF150593

Appendix 3 (continued).

Taxon	Collection Locality	Voucher Specimen	GenBank Accession No.
Lipocarpha maculata (Michx.) Torr.	Charlton County, Georgia	Reid and Carter 7742 (LSU)	KF150594
Lipocarpha micrantha (Vahl) G.C. Tucker	St. Charles Parish, Louisiana	Reid 7577 (LSU)	KF150595
Lipocarpha maculata (Michx.) Torr.	Charlton County, Georgia	Reid and Carter 7742 (LSU)	KF150594
Lipocarpha micrantha (Vahl) G.C. Tucker	St. Charles Parish, Louisiana	Reid 7577 (LSU)	KF150595
Oreobolus venezuelensis Steyerm.	----------	----------	DQ450479.1
Oxycaryum cubense (Poepp. & Kunth) Palla	Iberia Parish, Louisiana	Reid 7796 (LSU)	KF150596
Oxycaruym cubense (GB) (Submitted to GenBank as *Cyperus blepharoleptos* Steud.)	----------	----------	JX566741.1
Pycreus filicinus (Vahl) T. Koyama	Jefferson Parish, Louisiana	Reid 7632 (LSU)	KF150597
Pycreus flavescens (L.) P. Beauv. ex Rchb.	Caddo Parish, Louisiana	Reid 7576 (LSU)	KF150598
Pycreus lanceolatus (Poir.) C.B. Clarke	Iberville Parish, Louisiana	Reid 7698 (LSU)	KF150599
Pycreus macrostachyos (Lam.) J. Raynal	Corrientes, Argentina	Reid 7819 (LSU)	KF193576
Pycreus polystachyos (Rottb.) P. Beauv.	Hamilton County, Florida	Reid and Carter 7764 (LSU)	KF150600
Pycreus sanguinolentus (Vahl) Nees ex C.B. Clarke	Camden County, Georgia	Reid and Carter 7747 (LSU)	KF150601
Queenslandiella hyalina (Vahl) Ballard	Dade County, Florida	Carter 18737 (LSU)	KF150602
Rhynchospora chinensis Nees & Meyen ex Nees	----------	----------	AB261680.1
Schoenoplectus pungens (Vahl) Palla	----------	----------	DQ385591.1
Scleria muehlenbergii Steud.	Allen Parish, Louisiana	Reid 7288 (LSU)	KF150603

APPENDIX 4:
TAXA INCLUDED IN PHYLOGENETIC ANALYSIS EMPLOYING FIVE GENIC LOCI (CHAPTER 3).

Taxon Name	Voucher Specimen	GenBank Accession Number				
		ITS	*matK*	*ndhF*	*rpl32-trnL*	*trnH-psbA*
Calliscirpus brachythrix C.N. Gilmour, J.R. Starr, & Naczi	----------	N/A	JX074671	KJ513486	no data	no data
*Cyperus*sp. (*Pycreus*P. Beauv.)	Reid 8482	KX306827	KX369524	KX405840	no data	KX405822
Cyperus acuminatus Torr. & Hook.	Reid 6171	KF146652	KX369421	KX405843	KX405618	KX405722
Cyperus aggregatus (Argentina 7806)	Reid 7806	KF193566	KX369422	no data	KX405619	no data
Cyperus aggregatus (Louisiana)	Reid 7620	KF146653	KX369423	KX405844	KX405620	KX405723
Cyperus aggregatus (Willd.) Endl. (Argentina 7815) This sample was assigned the incorrect name of *Cyperus cayennensis* Willd. ex Link by Reid et al. (2014).	Reid 7815	KF150539	KX369430	no data	KX405625	KX405729
Cyperus alopecuroides Rottb.	Reid and Carter 8628	KX306829	KX369424	KX405845	no data	KX405724
Cyperus andinus Palla ex. Kük. (*C. seslerioides* Kunth)	Gonzalez 8114	KX306830	KX369425	KX405846	KX405621	KX405725
Cyperus articulatus L.	Reid 7487	KF150538	KX369427	KX405847	KX405622	KX405726
Cyperus blepharoleptos Steud.	Reid 7796	KF150596	KX369537	KX405949	KX405720	KX405834
Cyperus blodgettii Britton (*C. retrorsus* Chapm.)	Reid and Carter 8665	KX306832	KX369429	KX405849	KX405624	KX405728
Cyperus brevifolius (Rottb.) Hassk.	Reid and Carter 7755	KF150590	KX369530	KX405943	KX405713	KX405828
Cyperus cephalanthus (Texas)	Reid and Rosen 7510	KF193567	KX369434	KX405852	KX405627	KX405733
Cyperus cephalanthus (Louisiana)	Reid 7058	KF150540	KX369433	KX405851	KX405626	KX405730
Cyperus compressus (Louisiana)	Reid 7580	KF150541	KX369436	no data	KX405629	KX405734

Appendix 4 (continued).

Taxon Name	Voucher Specimen	GenBank Accession Number				
		ITS	*matK*	*ndhF*	*rpl32-trnL*	*trnH-psbA*
Cyperus compressus L. (Georgia)	Reid and Carter 7761	KF193575	KX369435	KX405853	KX405628	KX405735
Cyperus conceptionis Steud. (*C. rigens*J. Presl & C. Presl ssp. *rigens*)	Mihoc 3206 (CONC)	KX306863	KX369517	KX405929	no data	KX405813
Cyperus croceus Vahl (Florida)	Reid and Carter 8670	KX306835	KX369437	KX405854	KX405630	KX405738
Cyperus croceus Vahl (Louisiana)	Reid 7501	KF150543	KX369438	KX405855	KX405631	KX405737
Cyperus cuspidatus Kunth	Reid and Carter 7760	KF150544	KX369439	no data	KX405632	KX405739
Cyperus difformis L. (Louisiana)	Reid 7579	KF150545	KX369440	KX405856	KX405633	KX405740
Cyperus difformis (Mexico)	Gonzalez 8127	KX306836	KX369441	KX405857	KX405634	KX405741
Cyperus digitatus Roxb.	Reid and Rosen 7505	KF150546	KX369442	KX405858	KX405635	no data
Cyperus diminutus (8643)	Reid and Carter 8643	KX306838	KX369444	KX405860	KX405637	KX405743
Cyperus diminutus R. Carter, sp. nov. ined. (8635)	Reid and Carter 8635	KX306837	KX369443	KX405859	KX405636	KX405742
Cyperus distinctus Steud.	Reid and Carter 7744	KF150547	KX369445	KX405861	KX405638	KX405744
Cyperus *echinatus* "var. *sphaericus*"	Reid 7504	KF150549	KX369446	KX405862	KX405640	KX405746
Cyperus echinatus (L.) Alph. Wood (Typical)	Reid and Carter 8044	KF150548	KX369447	KX405863	KX405639	KX405745
Cyperus elegans (Mexico 8137)	Gonzalez 8137	KX306840	KX369449	KX405865	KX405642	KX405748
Cyperus elegans (Mexico 8140)	Gonzalez 8140	KX306839	KX369450	KX405866	KX405643	KX405749
*Cyperus elegans*L. (Louisiana)	Reid 7722	KF150550	KX369448	KX405864	KX405641	KX405747
Cyperus eragrostis Lam.	Reid 7514	KF150551	KX369451	KX405867	KX405644	KX405750
Cyperus erythrorhizos (south Louisiana)	Reid 7578	KF150552	KX369453	KX405869	KX405646	KX405752

Appendix 4 (continued).

Taxon Name	Voucher Specimen	GenBank Accession Number				
		ITS	*matK*	*ndhF*	*rpl32-trnL*	*trnH-psbA*
Cyperus erythrorhizos Muhl. (north Louisiana)	Reid 7530	KF193571	KX369452	KX405868	KX405645	KX405751
Cyperus esculentus L.	Gonzalez 8129	KX306841	KX369454	KX405870	KX405647	KX405753
Cyperus esculentus var. *leptostachyus* Boeckeler (included within *C. esculentus*)	Reid 7481	KF150553	KX369455	KX405871	KX405648	KX405754
*Cyperus esculentus*var. *macrostachyus* Boeckeler (included within *C. esculentus*)	Reid 7630	KF193572	KX369456	KX405872	KX405649	KX405755
Cyperus filicinus Vahl	Reid 7632	KF150597	KX369457	KX405873	KX405650	KX405756
Cyperus filiculmis (Louisiana)	Reid 7627	KF150554	KX369459	KX405875	KX405652	KX405757
*Cyperus filiculmis*Vahl (Florida)	Reid and Carter 8664	KX306842	KX369458	KX405874	KX405651	no data
Cyperus filiformis Sw.	Reid and Carter 8660	KX306843	To be submitted to GB	KX405876	KX405653	KX405758
Cyperus flavescens (Mexico)	Gonzalez 8115	KX306870	KX369538	KX405950	KX405654	KX405654
Cyperus flavescens L. (Louisiana)	Reid 7576	KF150598	KX369460	KX405877	KX405655	KX405759
Cyperus fuligineus Chapm.	Reid and Carter 8663	KX306844	KX369462	KX405879	KX405656	KX405835
Cyperus fuscus L.	Reid 7788	KF150555	KX369463	KX405880	KX405657	KX405761
Cyperus giganteus Vahl	Reid 8469	KX306845	KX369464	KX405881	KX405658	KX405762
Cyperus grayioides Mohlenbr.	Reid 7703	KF150556	KX369466	KX405883	KX405659	KX405764
Cyperus grayi Torr.	Reid and Carter 7757	KX306846	KX369465	KX405882	no data	KX405763
Cyperus haspan L.	Reid 7525	KF150557	KX369467	no data	KX405660	KX405765
Cyperus hortensis (Salzm. ex Steud.) Dorr	Reid and Carter 7754	KF150592	KX369532	KX405945	KX405715	KX405830
Cyperus hyalinus Vahl	Carter 18737	KF150602	KX369468	KX405884	KX405661	KX405766

Appendix 4 (continued).

Taxon Name	Voucher Specimen	GenBank Accession Number				
		ITS	*matK*	*ndhF*	*rpl32-trnL*	*trnH-psbA*
Cyperus hystricinus (Louisiana)	Reid 7705	KF193573	KX369470	KX405886	KX405663	KX405768
Cyperus hystricinus Fernald(Georgia)	Reid and Carter 8040	KX306847	KX369469	KX405885	KX405662	KX405767
Cyperus imbricatus Retz.	Reid 7807	KF150559	KX369471	KX405887	KX405664	KX405769
Cyperus impolitus (7901)	Reid 7901	KX306834	KX369431	no data	no data	KX405732
Cyperus impolitus Kunth (7838)	Reid 7838	KX306833	KX369432	KX405850	no data	KX405731
Cyperus incomtus Kunth	Reid 8491	KX306828	KX369420	KX405842	no data	KX405770
Cyperus intricatus Schrad.	Reid 8483	KX306864	KX369418	KX405841	KX405616	KX405823
Cyperus iria (Mexico)	Gonzalez 8131	KX306848	KX369473	KX405888	KX405666	KX405772
Cyperus iria L. (Argentina)	Reid 7799	KF150560	KX369472	no data	KX405665	KX405771
Cyperus kerstenii Boeckeler	----------	N/A	no data	no data	HQ705891	HQ705829
Cyperus lancastriensis Porter	Reid and Carter 8043	JX661627.1	KX369474	KX405889	KX405667	KX405774
Cyperus lanceolatus Poir. The names *Pycreus lanceolatus* (Poir.) C.B. Clarke and *P. macrostachyos* (Lam.) J. Raynal are transposed in table 1 of Reid et al. (2014)	Reid 7819	KF193576	KX369426	no data	KX405668	KX405775
Cyperus lecontei Torr. ex Steud.	Abbott 23732 (FLAS)	KF150562	KX369475	KX405890	KX405669	KX405776
Cyperus ligularis (Florida 23681)	Abbott 23681 (FLAS)	KF150563	KX369478	KX405893	KX405671	KX405778
Cyperus ligularis (Mexico)	Gonzalez 8139	KX306850	KX369477	KX405892	KX405672	KX405779
*Cyperus ligularis*L. (Florida 8634)	Reid and Carter 8654	KX306849	KX369476	KX405891	KX405670	KX405777
Cyperus lupulinus (Spreng.) Marcks	Reid 7711	KF150654	KX369479	KX405894	KX405673	KX405780

Appendix 4 (continued).

Taxon Name	Voucher Specimen	GenBank Accession Number				
		ITS	*matK*	*ndhF*	*rpl32-trnL*	*trnH-psbA*
Cyperus luzulae (L.) Retz.	Reid 7808	KF150565	KX369480	KX405895	KX405674	KX405781
Cyperus macrocephalus Liebm. (*C. odoratus* L. ssp. *odoratus*)	Reid 7161	KF150566	KX369481	KX405896	no data	KX405782
Cyperus macrostachyos Lam. The names *Pycreus lanceolatus* (Poir.) C.B. Clarke and *P. macrostachyos* (Lam.) J. Raynal are transposed in Table 1 of Reid et al. (2014).	Reid 7698	KF150599	KX369461	KX405878	no data	KX405760
Cyperus manimae Kunth	Gonzalez 8128	KX306851	KX369482	KX405897	KX405675	KX405783
Cyperus metzii (Hochst. ex Steud.) Mattf.	Reid and Carter 8629	KX306869	KX369533	KX405946	KX405716	KX405831
Cyperus neotropicalis Alain	Reid and Carter 7742	KF150594	KX369535	no data	KX405718	KX405832
Cyperus niger (8125)	Gonzalez 8125	KX306871	KX369539	KX405951	KX405721	KX405836
Cyperus niger Ruiz & Pav. (6338)	Reid 6338	KX306831	KX369428	KX405848	KX405623	KX405727
Cyperus ochraceus Vahl	Reid and Rosen 7512	KF150567	KX369485	KX405900	no data	no data
Cyperus odoratus (Louisiana)	Reid 7266	KF150569	KX369487	KX405902	KX405679	KX405788
Cyperus odoratus (Mexico)	Gonzalez 8136	KX306852	KX369488	KX405903	KX405680	KX405787
*Cyperus odoratus*L. (Argentina)	Reid 7798	KF150568	KX369486	KX405901	KX405678	KX405786
Cyperus ovatus (south Florida)	Reid and Carter 8658	KX306853	KX369490	KX405905	KX405682	no data
Cyperus ovatus Baldw. (north Florida)	Reid and Carter 7765	KF150570	KX369489	KX405904	KX405681	KX405789
Cyperus oxylepis Nees ex Steud.	Reid 7476	KF150571	KX369491	KX405906	KX405683	KX405790
Cyperus papyrus L.	----------	AY242048	no data	FM160537	HQ705892	HQ705830

Appendix 4 (continued).

Taxon Name	Voucher Specimen	GenBank Accession Number				
		ITS	*matK*	*ndhF*	*rpl32-trnL*	*trnH-psbA*
Cyperus pedunculatus (R. Br.) J. Kern	Reid and Carter 8666	KX306854	KX369492	KX405907	no data	KX405837
Cyperus pilosus Vahl	Reid 7575	KF150572	KX369493	KX405908	KX405684	KX405791
Cyperus planifolius (Miami)	Mears 5495	KF150573	KX369495	KX405909	KX405686	KX405793
Cyperus planifolius Rich. (Big Pine Key)	Reid and Carter 8662	KX306855	KX369494	Not yet submitted to GB	KX405685	KX405792
Cyperus plankii Britton ex Small (*C. retrorsus*Chapm.) This sample was labeled "*C. retrorsus* northwest Louisiana" in fig. 2 of Reid et al. (2014).	Reid 6144	KF193570	KX369506	KX405922	no data	KX405804
Cyperus plukenetii (Louisiana)	Reid 7464	N/A	Not yet submitted to GB	KX405911	KX405794	no data
Cyperus plukenetii Fernald (Georgia)	Reid and Carter 8039	KF150574	KX369496	KX405910	KX405687	KX405795
Cyperus polystachyos Rottb. subsp. *polystachyos* (7764)	Reid and Carter 7764	KF150600	KX369499	KX405913	no data	KX405796
*Cyperus polystachyos*subsp. *polystachyos* (8655)	Reid and Carter 8655	no data	KX369500	KX405914	KX405689	KX405797
*Cyperus polystachyos*var. *hahnianus* (Boeckeler) Kük. (*C. polystachyos* subsp. *polystachyos*)	Reid and Carter 8656	KX306856	KX369498	KX405912	KX405688	no data
Cyperus prolifer Lam.	Abbott 25162 (FLAS)	KF150575	KX369501	KX405915	KX405690	KX405798
Cyperus prolixus Kunth	Reid 7902	KF150576	KX369502	KX405916	KX405691	no data

Appendix 4 (continued).

Taxon Name	Voucher Specimen	GenBank Accession Number				
		ITS	*matK*	*ndhF*	*rpl32-trnL*	*trnH-psbA*
Cyperus pseudovegetus Steud.	Reid and Carter 8035	KF150577	KX369503	KX405917	KX405692	KX405799
*Cyperus reflexus*Vahl	Reid 8425	KX306826	KX369417	KX405839	KX405615	KX405821
Cyperus aff. *reflexus*Vahl	Reid 8488	KX306865	KX369419	KX405937	KX405617	KX405824
Cyperus refractus Engelm. ex Boeckeler	Carter 19848 (VSC)	KX306857	KX369504	KX405918	no data	KX405800
Cyperus regiomontanus Britton	Gonzalez 8135	KX306858	KX369505	KX405919	KX405693	KX405801
Cyperus retrorsus Chapm. var *nashi* (Britton) Fernald & Griscom (8636) (*C. retrorsus* Chapm.)	Reid and Carter 8636	no data	KX369483	KX405898	KX405676	KX405784
Cyperus retrorsus var. *nashi* Britton (8642) (*C. retrorsus*)	Reid and Carter 8642	no data	KX369484	KX405899	KX405677	KX405785
Cyperus retrorsus (North Carolina)	Carter 19850 (VSC)	KF150580	KX369507	KX405920	KX405694	KX405694
Cyperus retrorsus Chapm. (Louisiana)	Reid 7502	KF193569	KX369508	KX405921	KX405695	KX405805
Cyperus rigens J. Presl & C. Presl ssp. *rigens*	Reid 8428	KX306860	KX369511	KX405924	KX405698	KX405807
Cyperus rigens subsp. *rigens* (arenic variant)	Reid 7887	KX306859	KX369510	KX405923	KX405697	KX405806
Cyperus rigens subsp. *serrae* (Boeckeler) Pedersen	Reid 7868	KF193568	KX369512	KX405925	KX405699	KX405808
Cyperus rotundus (Louisiana)	Reid 8050	KX306861	KX369513	KX405926	KX405701	KX405809
*Cyperus rotundus*L. (Florida)	Abbott 23635 (FLAS)	KF150582	KX369514	KX405927	KX405700	KX405810
Cyperus sanguinolentus Vahl	Reid and Carter 7747	KF150601	KX369515	no data	KX405702	KX405811
Cyperus schomburgkianus Nees	----------	N/A	no data	no data	HQ705821	HQ705882
Cyperus sellowianus (Kunth) T. Koyama	Reid 7852	KF150593	KX369534	KX405947	KX405717	no data

Appendix 4 (continued).

Taxon Name	Voucher Specimen	GenBank Accession Number				
		ITS	*matK*	*ndhF*	*rpl32-trnL*	*trnH-psbA*
Cyperus seslerioides Kunth	Gonzalez 8113	no data	KX369516	KX405928	KX405703	KX405812
Cyperus sesquiflorus (Torr.) Mattf. & Kük.	Reid and Carter 7753	KF150591	KX369531	KX405944	KX405714	KX405829
Cyperus squarrosus L.	Reid 7554	KF150583	KX369518	KX405930	no data	KX405814
Cyperus stenolepis Torr. (*C. strigosus* L.)	Reid and Carter 8668	KX306862	KX369519	KX405931	KX405704	KX405815
Cyperus strigosus L. (Texas)	Reid and Rosen 7508	KF193574	KX369521	KX405933	KX405706	KX405817
Cyperus strigosus (Louisiana)	Reid 7581	KF150584	KX369520	KX405932	KX405705	KX405816
Cyperus subsqarrosus (Muhl.) Bauters	Reid 7577	KF150595	KX369536	KX405948	KX405719	KX405833
Cyperus surinamensis Rottb.	Reid 7478A	KF150585	KX369522	KX405934	KX405707	KX405818
Cyperus tetragonus Elliott	Reid and Carter 7752	KF150586	KX369523	KX405935	KX405708	KX405819
Cyperus thyrsiflorus Jungh. ex Schltdl.	Reid and Rosen 7511	KF150587	no data	KX405936	no data	KX405820
Cyperus virens (8126)	Gonzalez 8126	KX306867	KX369525	KX405939	KX405710	KX405826
Cyperus virens Michx. (8110)	Gonzalez 8110	KX306866	KX369526	KX405938	KX405709	KX405825
Cyperus waterlotii Cherm. (*C. cuspidatus*)	----------	N/A	no data	no data	HQ705885	HQ705825
Ficinia gracilis Schrad.	----------	AB685862	no data	no data	HQ705839	HQ705784
Ficinia nodosa (Rottb.) Goetgh.	----------	DQ385568	no data	GU075458	no data	KM462450
Fuirena robusta Kunth	Reid 7814	KF150588	KX369527	KX405940	KX405711	no data
Isolepis auklandica Hook. f.	----------	DQ385573	KJ513621	KJ513528	no data	no data
Isolepis carinata Hook. & Arn. ex Torr.	Reid 7962	KF150589	KX369528	KX405941	no data	no data
Isolepis cernua (Vahl) Roem. & Schult.	----------	DQ385576	JN895309	AM999934	no data	no data
Isolepis fluitans (L.) R.Br.	----------	DQ385579	JN893904	no data	HQ705838	HQ705783
Isolepis setacea (L.) R.Br.	----------	AB643644	JN895194	GU075460	no data	no data

Appendix 4 (continued).

Taxon Name	Voucher Specimen	GenBank Accession Number				
		ITS	*matK*	*ndhF*	*rpl32-trnL*	*trnH-psbA*
Karinia Mexicana (C.B. Clarke ex Britton) Reznicek & McVaugh	Gonzalez 8112 (CIIDIR and LSU)	KX306868	KX369529	KX405942	KX405712	KX405827
Schoenoplectus lacustris (L.) Palla	----------	KC677958	KC584943	AM999958	no data	KC584973
Schoenoplectus tabernaemontani (C.C. Gmel.) Palla	----------	DQ385592	HQ593435	KC678040	no data	no data
Scirpoides burkei (C.B. Clarke) Goetgh	----------	KM462294	no data	GU075457	no data	KM462439
Scirpoides holoschoenus (L.) Soják	----------	AB685867	KC584944	AM999964	HQ705837	HQ705782
Scleria muehlenbergii Steud.	Reid 7288	N/A	no data	XXXXX	seq submitted	no data
*Scleria verticillata*Muhl. ex Willd.	Reid 8651	KX306872	Not yet submitted to GB	XXXXX	seq submitted	KX405838

APPENDIX 5:
SPECIMENS INCLUDED IN MORPHOMETRIC STUDY OF THE *CYPERUS RIGENS* GROUP (CHAPTER 4).

Taxon	Herbarium	Collector & Number	Location
Cyperus cephalanthus	GH	Thieret 26368	Louisiana
Cyperus cephalanthus	LAF	Theiret 23018	Louisiana
Cyperus cephalanthus	LAF	Thieret 26368	Louisiana
Cyperus cephalanthus	LSU	Brown 9353	Louisiana
Cyperus cephalanthus	LSU	Correll 9435	Louisiana
Cyperus cephalanthus	NY	Langlois s.n.	Louisiana
Cyperus cephalanthus	VSC	Carter 10456	Louisiana
Cyperus cephalanthus	VSC	Carter 10476	Louisiana
Cyperus cephalanthus	VSC	Carter 10498	Louisiana
Cyperus cephalanthus	VSC	Carter 10500	Louisiana
Cyperus cephalanthus	VSC	Carter 10540	Louisiana
Cyperus cephalanthus	VSC	Carter 10541	Louisiana
Cyperus cephalanthus	VSC	Carter 10755	Louisiana
Cyperus cephalanthus	VSC	Carter 10759	Louisiana
Cyperus cephalanthus	VSC	Carter 10764	Louisiana
Cyperus cephalanthus	VSC	Carter 10766	Louisiana
Cyperus cephalanthus	VSC	Carter 10767	Louisiana
Cyperus cephalanthus	VSC	Carter 10771	Louisiana
Cyperus cephalanthus	VSC	Carter 10774	Louisiana
Cyperus cephalanthus	VSC	Carter 10780	Louisiana
Cyperus cephalanthus	VSC	Mears 5026	Louisiana
Cyperus cephalanthus	K	Drummond 455 (type)	Texas
Cyperus cephalanthus	VSC	Rosen 2950	Texas
Cyperus cephalanthus	VSC	Rosen 4239	Texas
Cyperus conceptionis	CONC	Acuna 9631	Chile
Cyperus conceptionis	CONC	Arriagada 107917	Chile
Cyperus conceptionis	CONC	Atnasio 14.443	Chile
Cyperus conceptionis	CONC	Barrientos 1648	Chile
Cyperus conceptionis	CONC	Gunckel 13.461	Chile
Cyperus conceptionis	CONC	Gunckel 14190	Chile
Cyperus conceptionis	CONC	Gunckel 17817	Chile
Cyperus conceptionis	CONC	Gunckel 39.890	Chile
Cyperus conceptionis	CONC	Julio Soa R. s.n.	Chile
Cyperus conceptionis	CONC	Kunkel 308	Chile
Cyperus conceptionis	CONC	Matthei 26954	Chile

Appendix 5 (continued)

Taxon	Herbarium	Collector and Number	Location
Cyperus conceptionis	CONC	Rodriguez and Baeza 2294A	Chile
Cyperus conceptionis	CONC	Rodriquez 1824	Chile
Cyperus conceptionis	CONC	Rudolph 9091	Chile
Cyperus conceptionis	CONC	Sparre 3606	Chile
Cyperus conceptionis	GH	Gunckel 5818	Chile
Cyperus conceptionis	NY	Pennell 12913	Chile
Cyperus impolitus	BA	Rodriguez 5413A	Argentina
Cyperus impolitus	CTES	Arbo et al. 6025	Argentina
Cyperus impolitus	CTES	Krapovickas et al 24063 A	Argentina
Cyperus impolitus	CTES	Krapovickas et al 24063 B	Argentina
Cyperus impolitus	GH	Barrela s.n.	Argentina
Cyperus impolitus	GH	Rodriguez 9615	Argentina
Cyperus impolitus	INTA	Fortunato 2386	Argentina
Cyperus impolitus	LSU	Reid 7838	Argentina
Cyperus impolitus	LSU	Reid 7901	Argentina
Cyperus impolitus	MO	Pedersen 10228	Argentina
Cyperus impolitus	NY	Pedersen 12957	Argentina
Cyperus impolitus	NY	Pedersen 8050	Argentina
Cyperus impolitus	NY	Schinini et al. 18868	Argentina
Cyperus impolitus	ICN	Hefler and Longhi-Wagner 388	Brazil
Cyperus impolitus	NY	Dusen 13624	Brazil
Cyperus impolitus	NY	Koyama 13786	Brazil
Cyperus impolitus	NY	Smith and Klein 10752	Brazil
Cyperus impolitus	NY	Smith and Klein 13888	Brazil
Cyperus impolitus	NY	Tsugaru & Otsuka B2267	Brazil
Cyperus impolitus	CTES	Schinini 5843	Paraguay
Cyperus impolitus	VSC	Schinini 26782	Paraguay
Cyperus oostachyus	BA	Krapovickas et al 16601	Argentina
Cyperus oostachyus	BA	Weber and Bachmann 45974	Argentina
Cyperus oostachyus	CORD	Hosseus 541	Argentina
Cyperus oostachyus	CORD	Kurtz 10534	Argentina
Cyperus oostachyus	CORD	Kurtz 3945	Argentina
Cyperus oostachyus	ICN	Hefler 430	Brazil
Cyperus oostachyus	NY	Pedersen 13857	Uruguay

Appendix 5 (continued)

Taxon	Herbarium	Collector and Number	Location
Cyperus rigens subsp. *rigens*	A	Pedersen 5374	Argentina
Cyperus rigens subsp. *rigens*	A	Pedersen 7740	Argentina
Cyperus rigens subsp. *rigens*	A	Pedersen 8713	Argentina
Cyperus rigens subsp. *rigens*	CORD	Lewis 1837	Argentina
Cyperus rigens subsp. *rigens*	CTES	Schulz 2219	Argentina
Cyperus rigens subsp. *rigens*	INTA	Krapovickas et al. 16601	Argentina
Cyperus rigens subsp. *rigens*	LP	Abbiatti and Claps 887	Argentina
Cyperus rigens subsp. *rigens*	LP	Hurrell et al. 1152	Argentina
Cyperus rigens subsp. *rigens*	LP	Rojas 8916	Argentina
Cyperus rigens subsp. *rigens*	ICN	Araujo 008	Brazil
Cyperus rigens subsp. *rigens*	ICN	Araujo 521	Brazil
Cyperus rigens subsp. *rigens*	ICN	Araujo 549	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hageland 13221	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hagelund 15041	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler 218	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler 303	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler 350	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler 356	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler 418	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler 461	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler 493	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler 603	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler 605	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler 608	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler 614	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler 623	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler and Longhi-Wagner 342	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler and Longhi-Wagner 365	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler and Longhi-Wagner 369	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler and Longhi-Wagner 372	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler and Longhi-Wagner 399	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler and Longhi-Wagner 403	Brazil
Cyperus rigens subsp. *rigens*	ICN	Hefler et al 450	Brazil

Appendix 5 (continued)

Taxon	Herbarium	Collector and Number #	Location
Cyperus rigens subsp. *rigens*	ICN	Longhi-Wagner and S. Miotto 3471	Brazil
Cyperus rigens subsp. *rigens*	ICN	Longhi-Wagner et al. 2451	Brazil
Cyperus rigens subsp. *rigens*	ICN	Nevez s.n.	Brazil
Cyperus rigens subsp. *rigens*	ICN	Wagner and Araujo 2145	Brazil
Cyperus rigens subsp. *rigens*	ICN	Wagner et al 2367	Brazil
Cyperus rigens subsp. *rigens*	NY	Dusen 8685	Brazil
Cyperus rigens subsp. *rigens*	NY	Longhi-Wagner and S. Miotto 2546	Brazil
Cyperus rigens subsp. *rigens*	A	Pedersen 9407	Paraguay
Cyperus rigens subsp. *rigens*	NY	Hassler 12681	Paraguay
Cyperus rigens subsp. *rigens*	NY	Pedersen 9478	Paraguay
Cyperus rigens subsp. *rigens*	NY	Zardini and Velazquez 24679	Paraguay
Cyperus rigens subsp. *rigens*	NY	Herter 1614c	Uruguay
Cyperus rigens subsp. *rigens* (arenic variant)	A	Caceres 393	Argentina
Cyperus rigens subsp. *rigens* (arenic variant)	CTES	Krapovickas and Cristol 14756	Argentina
Cyperus rigens subsp. *rigens* (arenic variant)	LSU	Reid 7887	Argentina
Cyperus rigens subsp. *serrae*	LSU	Reid 7868	Argentina
Cyperus rigens subsp. *serrae*	BA	Partridge 60043	Argentina
Cyperus rigens subsp. *serrae*	CONC	Barros 360	Argentina
Cyperus rigens subsp. *serrae*	MO	Bacigalpu 1577	Argentina
Cyperus rigens subsp. *serrae*	NY	Burkart 27.649	Argentina
Cyperus rigens subsp. *serrae*	B	Boeckeler s.n.	Brazil
Cyperus rigens subsp. *serrae*	ICN	Hefler 402 (A)	Brazil
Cyperus rigens subsp. *serrae*	K	Anonymous s.n.	Brazil
Cyperus rigens subsp. *serrae*	CTES	Pedersen 15891	Uruguay
Nonelement	NY	Beck 9977	Bolivia
Nonelement	CTES	Dombrowski 2480	Brazil
Nonelement	NY	Anderson 6735	Brazil
Nonelement	NY	Hunt 5805	Brazil
Nonelement	NY	Irwin 18569	Brazil
Nonelement	NY	Philcox and Fareira 4063	Brazil
Nonelement	NY	Rodrigues and Coelho 4299	Brazil

APPENDIX 6:
ANNOTATED CHECKLIST OF VASCULAR PLANTS DOCUMENTED FROM WET COASTAL PRAIRIES IN SOUTHWEST LOUISIANA.

Names are presented alphabetically by family and then scientific name within each family. Each scientific name is followed by the coefficient of conservatism (C-value), wetland indicator status if one has been assigned, and voucher specimen collector and number. Native species have positive C-values. Most specimens are deposited at LSU; for those specimens not deposited at LSU, the herbarium code follows the collector number in parentheses. A few species lack voucher specimens and are included on the basis of sight records and are so indicated. Species names preceded by a superscript "H" (^{H}) are included on the basis of older specimens and were not observed or collected during field work for this study. These species are considered historical members of the flora until they can be verified as extant. If the scientific name used is not accepted by USDA, NRCS (2015), the literature source for that same is given as the last annotation for that taxon.

ACANTHANTHACEAE
Justicia lanceolata (Chapm.) Small, 3, OBL, Reid 9231
Ruellia humilis Nutt., 8, FACU, Reid 9437

ACERACEAE
Acer rubrum L. var. *drummondii* (Hook. & Arn. ex Nutt.) Sarg., 1, Reid 9680

ALISMATACEAE
Echinodorus cordifolius (L.) Griseb., 2, OBL, Reid 9915
Sagittaria graminea Michx., 4, OBL, Reid 9162
Sagittaria lancifolia L., 3, OBL, Reid 7300
Sagittaria papillosa Buch., 4, OBL, Urbatsch 11384
Sagittaria platyphylla (Engelm.) J.G. Sm., 1, OBL, Reid sight record

AMARANTHACEAE
Alternanthera philoxeroides (Mart.) Griseb, -1, OBL, Reid 9202

ANACARDIACEAE
Toxicodendron radicans (L.) Kuntze, 1, FAC, Reid 9923

APIACEAE
Centella erecta (L.f.) Fernald, 5, FACW, Reid 9456
Cicuta maculata L., 3, OBL, Reid 9166
Eryngium hookeri Walp., 2, FACW, Allain 4972
Eryngium yuccifolium Michx., 9, FAC, Allain 1492 (USGS)
Hydrocotyle umbellata L., 1, OBL, Reid 9221
Limnosciadium pumilum (Engelm. & A. Gray) Mathias & Constance, 4, OBL, Reid 9167
Ptilimnium capillaceum (Michx.) Raf., 3, OBL, Urbatsch 11378
Ptilimnium texense J.M. Coulter & Rose, 7, Brown 20872 (Feist 2010)

APOCYNACEAE
Amsonia rigida Shuttlw. ex Small, 7, FACW, Urbatsch 11349
Trachelospermum difforme (Walter) A. Gray, 2, FACW, Doffitt s.n.

AQUIFOLIACEAE
Ilex decidua Walter, 2, FACW, Reid 9834
Ilex opaca Aiton, 1, FAC, Reid 9761
Ilex vomitoria Aiton, 2, FAC, Reid 9735

ARECACEAE
Sabal minor (Jacq.) Pers., 3, FACW, Reid 6807

ASCLEPIADACEAE
Asclepias lanceolata Walter, 8, OBL, Doffitt 3372
Asclepias longifolia Michx. var. *hirtella* (Pennell) B.L. Turner, 7, Reid 9229 (Turner 2009)
Asclepias obovata Elliott, 8, Reid 9832
Asclepias viridis Walter, 4, Reid 9663

ASTERACEAE
Acmella oppositifolia (Lam.) R.K. Jansen var. *repens* (Walter) R.K. Jansen, 1, FACW, Reid 9749
Ambrosia psilostachya DC., 3, FAC, Reid 9681
Anthemis cotula L., 0, FACU, Reid 9203
Arnoglossum ovatum (Walter) H. Rob., 8, FACW, Reid 8919
Baccharis angustifolia Michx., 3, FACW, Reid 7301
Baccharis halimifolia L., 2, FAC, Reid 9740
Bidens aristosa (Michx.) Britt., 5, FACW, Reid 9734
Boltonia asteroides (L.) L'Her, 4, FACW, Reid 9719
Chromolaena ivifolia (L.) King & H.E. Robins., 5, Reid 7272
H*Chrysopsis mariana* (L.) Ell., 8, UPL, Brown 8623
Chrysopsis pilosa Nutt., 7, Reid 9753
Cirsium horridulum Michx., 2, FAC, Reid 9146
Conoclinium coelestinum (L.) DC., 4, FAC, Reid 9679
Conyza bonariensis (L.) Cronquist, 0, FACU, Reid 9855
Conyza candensis (L.) Cronquist var. *pusilla* (Nutt.) Cronquist, 2; Reid 9699
Coreopsis tinctoria Nutt., 3, FAC, Reid 9537
H*Echinacea pallida* (Nutt.) Nutt., 9, Brown 9293
Eclipta prostrata (L.) L., 1, FACW, Reid 9514
Erechtites hieraciifolius (L.) Raf. ex DC., 1, FAC, Reid 9238
Erigeron tenuis Torr. & A. Gray, 3; Urbatsch 11343.5
Eupatorium capillifolium (Lam.) Small, 1, FACU; Reid 9733
Eupatorium compositifolium Walter, 2, FAC: Reid 9729

Eupatorium hyssopifolium L., 5, Reid 8715
Eupatorium rotundifolium L., 7, FAC, Reid 9415
Eupatorium semiserratum DC., 6, FACW, Reid 8709
Eupatorium serotinum Michx., 2, FAC, Reid 9728
Euthamia gymnospermoides Greene, 6, FAC, Reid 9686
Euthamia leptocephala (Torr. & A. Gray) Greene ex Porter & Britton, 5, FACW, Reid 9676
Gaillardia aestivalis (Walt.) H. Rock var. *aestivalis*, 8, Reid 8991
Gamochaeta coarctata (Willd.) Kerguelen, 0, Reid 9160
Helenium amarum (Raf.) H. Rock, 1, FACU, Reid 9500
Helenium drummondii H. Rock, 6, OBL, Reid 9790
Helenium flexuosum Raf., 5, FACW, Reid 9753
Helianthus angustifolius L., 6, FACW, Reid 9564
Helianthus mollis Lam., 10, Reid 7655
Hymenopappus artemisiifolius DC., 8, Reid 9157
Hypochaeris microcephala (Sch. Bip.) Cabrera, 0, Reid 9199
Iva angustifolia Nutt. ex DC., 2, Reid 9674
Iva annua L., 1, FAC, Reid 9718
Krigia caespitosa (Raf.) K.L. Chambers, 1, FAC, Reid 9769
Liatris acidota Engelm. ex A. Gray, 9, FACW, Reid 9425
Liatris pycnostachya Michx., 9, FACU, Reid 7669
H*Marshallia caespitosa* Nutt. var. *caespitosa*, 9, Brown 8951
Mikania scandens (L.) Willd., 1, FACW, Reid 9552
Oligoneuron nitidum (Torr. & A. Gray) Small [Syn *Solidago nitida* Torr. & A. Gray], 7, Brown 9725
Packera tomentosa (Michx.) C. Jeffrey, 7, FACU, Reid 9101
H*Pityopsis graminifolia* (Michx.) Nutt., 9, UPL, Brown 8624
Pluchea baccharis (Mill.) Pruski [Syn *Pluchea rosea* Godfrey], 4, FACW, Reid 9748 (Pruski 2005)
Pluchea foetida (L.) DC., 5, OBL, Reid 9494
Pseudognaphalium luteoalbum (L.) Hilliard & B.L. Burtt, 0, FAC, Reid
Pyrrhopappus carolinianus (Walter) DC., 2, Reid 9233
Rudbeckia hirta L., 6, FACU, Reid 9452
Rudbeckia texana (Perdue) P. Cox & Urbatsch, 10, Reid 8918
Silphium gracile A. Gray, 8, Reid 9414
Solidago altissima L., 2, FACU, Reid 9675
Solidago odora Ait., 10, Reid 9670
Solidago rugosa P. Mill., 7, FAC, Urbatsch 12109
Solidago sempervirens L. var. mexicana (L.) Fern., 6, FACW, Reid 9752
Solidago speciosa Nutt. var. *rigidiuscula* Torr. & A. Gray, 8, Cocks s.n.
Solidago tortifolia Ell., 8, Reid 8994
Symphyotrichum divaricatum (Nutt.) G.L. Nesom, 2, OBL, Reid 9717
Symphyotrichum dumosum (L.) G.L. Nesom, 4, FAC, Reid 8708
Symphyotrichum lanceolatum (Willd.) G.L. Nesom, 3, FACW, Reid 9688

Symphyotrichum ontarionis (Weigand) G.L. Nesom, 6, FAC, Gilmore 3453
[H]*Symphyotrichum pratense* (Raf.) G.L. Nesom, 7, Brown 8637
Symphyotrichum racemosum (Elliott) G.L. Nesom, 4, FACW, Reid 9689
Symphyotrichum subulatum (Michx.) G.L. Nesom, 2, OBL, Reid 5514
Vernonia gigantea (Walt.) Trel., 2, FAC, Reid 6801
Vernonia missurica Raf., 6, FAC, Reid 8139
[H]*Vernonia texana* (A. Gray) Small, 8, FACU, Correll 9580
Xanthium strumarium L., 1, FAC, Reid 9551

BIGNONIACEAE
Bignonia capreolata L., 1, FAC, Reid 9613
Campsis radicans (L.) Seem. ex Bureau, 1, FAC, 9606

BORAGINACEAE
Heliotropium curassavicum L., 3, OBL, Reid 9852
Heliotropium procumbens Mill., 2, FACW, Reid 9561

BRASSICACEAE
Capsella bursa-pastoris (L.) Medik., 0, FACU, Reid 9152
Cardamine parviflora L., 1, FACU, Reid 9148
Lepidium virginicum L., 1, UPL, Reid 9296

CALLITRICHACEAE
Callitriche terrestris Raf., 1, FACW, Reid 9110

CAMPANULACEAE
Lobelia appendiculata A. DC., 7, FAC, Reid 9158
Lobelia puberula Michx., 7, FACW, Reid 9704
Triodanis perfoliata (L.) Nieuwl., 2, FACU, Urbatsch 11379

CAPRIFOLIACEAE
Lonicera japonica Thunb., -2, FACU, Reid 9433
Sambucus nigra L. ssp. *canadensis* (L.) Bolli, 1, FACW, Reid 9434
Viburnum dentatum L., 2, FAC, Reid 9280

CARYOPHYLLACEAE
Cerastium glomeratum Thuill., 0, FACU, Reid 9770
Sagina decumbens (Elliott) Torr. & A. Gray, 1, FACU, Reid 9126
Silene gallica L., 0, Reid 9191
Spergularia salina J. Presl & C. Presl, 2, OBL, Reid 9186

CLUSIACEAE
Hypericum densiflorum Pursh, 7, FACW, Reid 8915
Hypericum drummondii (Grev. & Hook.) Torr. & A. Gray, 4, FACU, Reid 9738
Hypericum galioides Lam., 7, OBL, Brown 5867
Hypericum gymnathum Engelm. & A. Gray, 4, FACW, Urbatsch 11367
Hypericum hypericoides (L.) Crantz, 4, FAC, Reid 9439

COMMELINACEAE
Commelina erecta L., 5, FACU, Reid 9780
Tradescantia hirsutiflora Bush, 6, Reid 9236

CONVOLVULACEAE
Calystegia sepium (L.) R. Br., 3, FAC, Reid 9291
Dichondra carolinensis Michx., 1, FAC, Reid 9277
Ipomoea cordatotriloba Dennst., 1, FACU, Reid 9609
Ipomoea sagittata Poir., 6, FACW, Doffitt 3372

CUCURBITACEAE
Cucumis melo L., 0, Reid 9598
Melothria pendula L., 1, Reid 9612

CUPRESSACEAE
Juniperus virginiana L., 1, FACU, Reid 9615

CUSCUTACEAE
Cuscuta pentagona Engelm., 1, Reid 9906

CYPERACEAE
Carex alata Torr., 4, OBL, Reid 6500
Carex annectens (E.P. Bicknell) E.P. Bicknell, 3, FACW, Mayfield 2766
Carex aureolensis Steud., 2, OBL, Reid 9282
Carex complanata Torr. & Hook., 4, FAC, Rosen 7016
Carex flaccosperma Dewey, 3, FACW, Reid 8807
Carex longii Mack., 3, OBL, Reid 9183
Carex meadii Dewey, 9, FAC, Rosen 7015
Carex microdonta Torr. & Hook., 9, FACW, Reid 7388
Carex triangularis Boeckeler, 2, FACW, Reid 7073
Carex verrucosa Muhl., 7, OBL, Reid 8817
Cladium mariscus (L.) Pohl var. *jamaicense* (Crantz) Kük., 6, OBL, Reid sight record
Cyperus aggregatus (Willd.) Endl., 2, FAC, Reid 9533
Cyperus articulatus L., 2, OBL, Reid 9286
Cyperus brevifolius (Rottb.) Endl. ex Hassk. [Syn *Kyllinga brevifolia* Rottb.], 1, FACW, Reid 9358 (Govaerts et al. 2016)
Cyperus cephalanthus Torr. & Hook., 9, Reid 6105
Cyperus drummondii Torr. & Hook., 9, OBL, Reid 7308
Cyperus echinatus (L.) Alph. Wood, 6, FAC, Reid 9821
Cyperus entrerianus Boeckeler, -2, FACW, Reid 9510
Cyperus esculentus L., 1, FAC, Reid 8928
Cyperus filicinus Vahl, 1, OBL, Reid 7254
Cyperus haspan L., 5, OBL, 9351

Cyperus hemidrummondii Goetgh. [Syn *Lipocarpha drummondii* (Nees) G. C. Tucker], 1, OBL, Reid 8801 (Govaerts et al. 2016)
Cyperus hortensis (Salzm. ex Steud.) Dorr [Syn *Kyllinga pumila* Michx.], 1, FACW, Reid s.n. (Govaerts et al. 2016)
Cyperus iria L., 0, FACW, Reid 9910
Cyperus macrostacyos Lam. [Syn *Cyperus flavicomus* Michx.], 1, FACW, Reid 8964 (Govaerts et al. 2016)
Cyperus odoratus L., 1, FACW, Reid 7265
Cyperus pilosus Vahl, -1, FACW, Reid 9854
Cyperus polystachyos Rottb., 1, FACW, Reid 9935
Cyperus pseudovegetus Steud., 2, FACW, Reid 9228
Cyperus reflexus Vahl var. *fraternus* (Kunth) Kuntze, 5, FAC, Reid 8940 (VSC) (Denton 1978)
Cyperus retrorsus Chapm., 4, FACU, Reid 9363
Cyperus sanguinolentus Vahl, -1, FACW, Reid 9911
Cyperus sesquiflorus (Torr.) Mattf. & Kük. [Syn *Kyllinga odorata* Vahl], 1, FACW, Reid 9359 (Govaerts et al. 2016)
Cyperus strigosus L., 3, FACW, Reid 9934
Cyperus virens Michx., 1, FACW, Reid 9270
Eleocharis acicularis (L.) Roem. & Schult., 2, OBL, Reid 9172
Eleocharis macrostachya Britton, 3, Urbatsch 11365
Eleocharis microcarpa Torr., 2, OBL, Urbatsch 11370
Eleocharis montana (Kunth) Roem. & Schult., 4, OBL, Reid 9230
Eleocharis montevidensis Kunth, 3, FACW, Urbatsch 11369
Eleocharis obtusa (Willd.) Schult., 1, OBL, Reid 9306
Eleocharis olivacea Torr. var. *olivacea*, 2, OBL, Reid 9931
Eleocharis parvula (Roemer & Schult.) Link ex Bluff, Nees, & Schauer, 2, OBL, Reid 8802
Eleocharis quadrangulata (Michx.) Roem. & Schult., 4, OBL, Reid 9441
Eleocharis tenuis (Willd.) J.A. Schultes var. *verrucosa* (Svenson) Svenson, 4, Reid 8805
Eleocharis tuberculosa (Michx.) Roem. & Schult., 6, OBL, Reid 8826
Fimbristylis autumnalis (L.) Roem. & Schult., 1, OBL, Reid 9388
Fimbristylis caroliniana (Lam.) Fernald, 6, OBL, Reid 9539
Fimbristylis castanea (Michx.) Vahl, 4, OBL, Urbatsch 11375
Fimbristylis dichotoma (L.) Vahl, 1, OBL, Reid 9532
Fimbristylis littoralis Gaudich. [Syn *Fimbristylis miliacea* (L.) Vahl], 0, OBL, Reid 9530
Fimbristylis puberula (Michx.) Vahl, 6, OBL, Reid 9326
Fuirena breviseta (Coville) Coville, 6, OBL, Reid 9443
Isolepis carinata Hook. & Arn. ex Torr., 1, FACW, Reid 9130
Isolepis cernua (Vahl) Roem. & Schult., 3, OBL, 9808
Rhynchospora caduca Elliott, 6, OBL, Reid 9700
Rhynchospora careyana Fernald, 8, OBL, Reid 8995
Rhynchospora colorata (L.) H. Pfeiff., 5, FACW, Reid 9438
Rhynchospora elliottii A. Dietr., 7, FACW, Reid 9339
Rhynchospora fascicularis (Michx.) Vahl, 7, FACW, Reid 9427

Rhynchospora filifolia A. Gray, 7, FACW, Reid 9413
Rhynchospora globularis (Chapm.) Small var. *globularis*, 6, Reid 9176
Rhynchospora globularis (Chapm.) Small var. *pinetorum* (Britton & Small) Gale, 7, Reid 9453
Rhynchospora glomerata (L.) Vahl, 6, OBL, Reid 9447
Rhynchospora gracilenta A. Gray, 8, OBL, Urbatsch 11383
Rhynchospora inexpansa (Michx.) Vahl, 4, FACW, Reid 9336
Rhynchospora macrostachya Torr. ex A. Gray, 2, OBL, Reid 9449
Rhynchospora microcarpa Baldw. ex A. Gray, 7, OBL, Reid 6498
Rhynchospora nitens (Vahl) A. Gray, 4, OBL, Reid 9933
Rhynchospora perplexa Britton, 7, OBL, Reid 9387
Rhynchospora plumosa Elliott, 8, FACW, Rosen 7007
Rhynchospora pusilla Chapm. ex M.A. Curtis, 7, FACW, Reid 9217
Rhynchospora rariflora (Michx.) Elliott, 7, OBL, Reid 9165
Rhynchospora recognita (Gale) Kral, 8, FACW, Reid 9360
Scleria bellii LeBlond, 7, Reid 6539 (LeBlond et al. 2015)
Scleria georgiana Core, 8, FACW, Reid 9429
Scleria muehlenbergii Steud., 7, OBL, Reid 7665
Scleria pauciflora Muhl. ex Willd. var. *pauciflora*, 8, Reid 9246
Scleria verticillata Muhl. ex Willd., 7, OBL, Reid sight record

DENNSTAEDTIACEAE
Pteridium aquilinum (L.) Kuhn, 7, FACU, Reid 9135

DROSERACEAE
Drosera brevifolia Pursh, 5, OBL, Reid 9771

EBENACEAE
Diospyros virginiana L., 2, FAC, Reid 9856

EUPHORBIACEAE
Acalypha gracilens A. Gray, 2, FAC, Reid 9362
Chamaesyce serpens (Kunth) Small, 1, FAC, Reid 8375
Chamaesyce serpyllifolia (Pers.) Small, 1, Reid 9524
Croton capitatus Michx. var. *lindheimeri* (Engelm. ex A. Gray) Mull. Arg., 1, Reid 9526
Croton michauxii G.L. Webster var. *ellipticus* (Willd.) van Ee & P.E. Berry, 7, Reid 9858
Euphorbia bicolor Engelm. & Gray, 7, Reid 8365
Euphorbia corollata L., 9, Reid 9831
Phyllanthus urinaria L., 0, FAC, Reid 9383
Stillingia sylvatica Garden ex L., 8, Reid 8920
Triadica sebifera (L.) Small, -3, FAC, Reid 9529

FABACEAE
Baptisia alba (L.) Vent., 7, FACU, Reid 9168
Baptisia bracteata Muhl. ex Elliott var. laevicaulis (A. Gray ex Canby) Isely, 8, Urbatsch 11357

Centrosema virginiana (L.) Benth., 4, Reid 9492
Chamaecrista fasciculata (L.) Benth., 4, FACU, Reid 9440
Desmodium sessilifolium (Torr.) Torr. & A. Gray, 7, Reid 7668
Galactia volubilis (L.) Britt., 4, FACU, Reid 9525
Lathyrus pusillus Elliott, 1, FAC, Reid 5516
Mimosa hystricina (Sm. ex Britt. & Rose) B.L. Turner, 8, Reid 8861
Mimosa strigillosa Torr. & A. Gray, 2, FAC, Reid 9328
Neptunia lutea (Leavenworth) Benth., 7, FACU, Brown 5869
Neptunia pubescens Benth., 5, FAC, Reid 9828
Orbexilum simplex (Nutt. ex Torr. & Gray) Rydb., 8, FAC, Urbatsch 11340
Senna obtusifolia (L.) Irwin & Barneby, 1, FACU, Reid 9511
Sesbania drummondii (Rydb.) Cory, 1, FACW, Reid 9860
Sesbania vesicaria (Jacq.) Elliott, 1, FAC, Reid 9520
Strophostyles leiosperma (Torr. & A. Gray) Piper, 5, Reid 9538
Strophostyles umbellata (Muhl. ex Willd.) Britt., 5, FAC, Reid 9522
Tephrosia onobrychoides Nutt., 10, Reid 9224
Trifolium repens L., 0, FACU, Reid 9805
Trifolium resupinatum L., -1, FACU, Reid 9147
Vicia ludoviciana Nutt., 1, FACU, Reid 9154
Vicia villosa Roth, 0, Reid 5521
Vigna luteola (Jacq.) Benth., 2, FACW, Reid 9513

FAGACEAE
Quercus nigra L., 1, FAC, Reid 9614
Quercus virginiana Mill., 1, FACU, Reid 9595

GENTIANACEAE
Centaurium pulchellum (Sw.) Druce, 0, FACU, Urbatsch 11342
Eustoma exaltatum (L.) Salisb. ex G. Don ssp. *exaltatum*, 5, FACW, Reid 9416
Sabatia campanulata (L.) Torr., 7, FACW, Reid 8924
Sabatia campestris Nutt., 5, FACU, Urbatsch 11344
Sabatia dodecandra (L.) Britton, Sterns & Poggenb. var. *foliosa* (Fern.) Wilbur, 8, OBL, Reid 8019

GERANIACEAE
Geranium carolinianum L., 1, Reid 9350

HALORAGACEAE
Myriophyllum pinnatum (Walter) Britton, Sterns & Poggenb., 4, OBL, Reid 9299
Proserpinaca palustris L., 5, OBL, Reid 9164
Proserpinaca pectinata Lam., 6, OBL, Reid 9445

HAMAMELIDACEAE
Liquidambar styraciflua L., 1, FAC, Reid 9758

HYDROPHYLLACEAE
Hydrolea ovata Nutt. ex Choisy, 6, OBL, Reid 9442

IRIDACEAE
Alophia drummondii (Graham) R.C. Foster, 9, FACU, Reid sight record
Iris brevicaulis Raf., 4, OBL, Allain 4971
Iris giganticaerulea Small, 3, OBL, Reid 9151
Sisyrinchium atlanticum E.P. Bicknell, 5, FACW, Urbatsch 11352
Sisyrinchium biforme E.P. Bicknell, 5, FAC, Reid 9133
Sisyrinchium langloisii Greene, 4, Reid 9121
Sisyrinchium rosulatum E.P. Bicknell, 1, FAC, Reid 9240
[H]*Sisyrinchium sagittiferum* E.P. Bicknell, 3, FAC, Brown 18798

JUNCACEAE
Juncus biflorus Elliott, 4, FACW, Urbatsch 11360
Juncus brachycarpus Engelm., 4, FACW, Urbatsch 11372
Juncus bufonius L., 1, FACW, Reid 9195
Juncus dichotomus Elliott, 4, FACW, Reid 9180
Juncus diffusissimus Buckley, 1, FACW, Reid 9169
*Juncus dudley*i Wiegand, 3, FACW, Reid 9190
Juncus effusus L., 1, OBL, Reid 9173
Juncus elliottii Chapm., 4, OBL, Reid 9161
Juncus interior Wiegand, 4, FACU, Reid 9265
Juncus nodatus Coville, 5, OBL, Reid 9269
Juncus repens Michx., 4, OBL, Urbatsch 11385
Juncus validus Coville, 2, FACW, Reid 9380

LAMIACEAE
Hedeoma hispida Pursh, 2, Reid 9803
Hyptis alata (Raf.) Shinners, 7, OBL, Reid 9382
Monarda punctata L., 6, FACU, Reid 8142
Physostegia intermedia (Nutt.) Engelm. & Gray, 5, FACW, Reid 9171
Physostegia virginiana (L.) Benth., 7, FACW, Reid 9709
Prunella vulgaris L., 3, FAC, Urbatsch 11347
Pycnanthemum tenuifolium Schrad., 8, FACW, Reid 8975
Salvia azurea Michx. ex Lam., 10, Reid 9568
Salvia lyrata L., 3, FACU, Reid 9802
Scutellaria integrifolia L., 9, FAC, Reid 9235
Scutellaria parvula Michx., 8, FACU, Reid 9120

LAURACEAE
Sassafras albidum (Nutt.) Nees, 4, FACU, Reid 9347

LENTIBULARIACEAE
Pinguicula pumila Michx., 9, OBL, Reid 9177

LILIACEAE
[H]*Aletris farinosa* L., 9, FAC, Featherman s.n.
Allium canadense L. var. *mobilense* (Regel) Ownbey, 7, Reid 9807
Cooperia drummondii Herb. [Syn *Zephyranthes chlorosolen* (Herb.) D. Dietr.], 6, FACU, Reid 5621
Hymenocallis liriosme (Raf.) Shinners, 3, OBL, Reid 9205
Hypoxis wrightii (Baker) Brackett, 8, FACW, Reid 9329
Nothoscordum bivalve (L.) Britton, 4, FACU, Reid 9668

LINACEAE
Linum medium (Planch.) Britton var. *texanum* (Planch.) Fernald, 5, Reid 9234

LOGANIACEAE
Gelsemium sempervirens (L.) W.T. Aiton, 2, FAC, Reid 6825
Mitreola petiolata (J.F. Gmel.) Torr. & A. Gray, 5, FACW, Reid 9292
Mitreola sessilifolia (J.F. Gmel.) G. Don, 5, FACW, Reid 9411

LYGODIACEAE
Lygodium japonicum (Thunb.) Sw., -2, FAC, Reid 9345

LYTHRACEAE
Cuphea carthagenensis (Jacq.) J.F. Macbr., -1, FACW, Reid 9348
Lythrum alatum Pursh var. *lanceolatum* (Elliott) Torr. & A. Gray ex Rothr., 5, OBL, Reid 8913
Lythrum lineare L., 3, OBL, Reid 7258
Rotala ramosior (L.) Koehne, 1, OBL, Reid 9912

MALVACEAE
Hibiscus aculeatus Walter, 8, FACW, Reid 9542
Hibiscus lasiocarpos Cav., 4, OBL, Reid 8932
Hibiscus leucophyllus Shiller [Syn *Hibiscus lasiocarpos* Cav.], 6, OBL, Reid 9333 (Shiller 1960)
Kosteletzkya virginica (L.) C. Presl ex A. Gray, 3, OBL, Reid 9331
Sida rhombifolia L., 1, FACU, Reid 9459

MELASTOMATACEAE
Rhexia mariana L., 7, FACW, Reid 9241
Rhexia virginica L., 8, FACW, Reid sight record

MYRICACEAE
Morella cerifera (L.) Small, 1, FAC, Reid 9737

NELUMBONACEAE
Nelumbo lutea Willd., 1, OBL, Reid 9920

OLEACEAE
Ligustrum sinense Lour., -2, FAC, Reid 9755

ONAGRACEAE
Ludwigia grandiflora (Michx.) Greuter & Burdet, 0, OBL, Reid 9288
Ludwigia hirtella Raf., 7, FACW, Reid 9337
Ludwigia linearis Walt., 6, OBL, Reid 7681
Ludwigia microcarpa Michx., 6, OBL, Reid 9907
Ludwigia octovalvis (Jacq.) P.H. Raven, 1, OBL, Reid 9926
Ludwigia palustris (L.) Elliott, 1, OBL, Reid 9298
Ludwigia peploides (Kunth) P.H. Raven, 1, OBL, Reid 9928
Oenothera filiformis (Small) W.L. Wagner & Hoch [Syn *Gaura longiflora* Spach], 5, Reid 7656
H*Oenothera grandis* (Britt.) Smyth, 5, Brown 8952
H*Oenthera heterophylla* Spach ssp. *heterophylla*, 7, Correll 9586
Oenothera lindheimeri (Engelm. & A. Gray) W.L. Wagner & Hoch [Syn *Gaura lindheimeri* Engelm. & A. Gray], 6, Reid 9714

ORCHIDACEAE
Spiranthes praecox (Walter) S. Watson, 5, FACW, Reid 9205
Spiranthes vernalis Engelm. & A. Gray, 4, FACW, Urbatsch 11381

OXALIDACEAE
Oxalis dillenii Jacq., 1, FACU, Reid 9114
Oxalis violacea L., 5, Reid 9117

PASSIFLORACEAE
Passiflora incarnata L., 3, Reid 9432

PHYTOLACCACEAE
Phytolacca americana L., 1, FACU, Reid 9346

PINACEAE
Pinus taeda L., 1, FAC, Reid 9751

PLANTAGINACEAE
Plantago virginica L., 1, FACU, Reid 9192

POACEAE
Agrostis elliottiana Schult., 4, FACU, Reid 9129
Agrostis hyemalis (Walter) Britton, Sterns & Poggenb., 3, FAC, Reid 9198

Andropogon capillipes Nash [Syn *Andropogon virginicus* L. var. *glaucus* Hack.], 5, FAC, Reid 8722

[H]*Andropogon gerardii* Vitman, 10, FAC, Brown 8660

Andropogon glomeratus (Walter) Britton, Sterns & Poggenb., 3, FACW, Reid 8724

Andropogon ternarius Michx., 7, FACU, Reid 9678

Andropogon virginicus L., 3, FAC, Reid 8730

Anthaenantia texana Kral (Kral 2004), 7, Reid 8707

Aristida longespica Poir. var. *longespica*, 3, Reid 9604

Aristida oligantha Michx., 3, Brown 8641

Aristida purpurascens Poir. var. *purpurascens*, 6, Reid 9621

Axonopus fissifolius (Raddi) Kuhlm., 1, FACW, Reid 9521

Axonopus furcatus (Flüggé) Hitchc., 1, OBL, Reid 7276

Bothriochloa longipaniculata (Gould) Allred & Gould, 3, Reid 8875

Briza minor L., 0, FAC, Reid 9141

Bromus catharticus Vahl, 0, Reid 9153

Chrysopogon pauciflorus (Chapm.) Benth. ex Vasey, 5, FACU, Reid 8960

Coelorachis cylindrica (Michx.) Nash, 9, FAC, Allain 1704

Coleataenia anceps (Michx.) Soreng var. *anceps* [Syn *Panicum anceps* Michx.], 4, Reid 9591 (Soreng 2010)

Coleataenia anceps var. *rhizomata* (A.S. Hitchc. & Chase) Soreng [Syn *Panicum anceps* Michx.], 4, Reid 9549 (Soreng 2010)

Coleataenia longifolia (Torr.) Soreng ssp. *longifolia* [Syn *Panicum rigidulum* Bosc ex Nees var. *pubescens* (Vasey) LeLong], 5, Reid 9922 (Soreng 2010)

Coleataenia rigidula (Bosc ex Nees) LeBlond ssp. *rigidula* [Syn *Panicum rigidulum* var. *rigidulum*], 4, Reid 9550 (Weakley et al. 2011)

Coleataenia stipitata (Nash) LeBlond [Syn *Panicum rigidulum* var. *elongatum* (Pursh) LeLong], 4, FACW, Reid 9421 (Weakley et al. 2011)

Cynodon dactylon (L.) Pers., -2, FACU, Reid 9754

Dichanthelium aciculare (Desv. ex Poir.) Gould & C.A. Clark, 6, FACU, Reid 9534

Dichanthelium acuminatum (Sw.) Gould & C.A. Clark var. *acuminatum*, 5, Reid 9835

Dichanthelium columbianum (Scribn.) Freckmann [Syn *Dichanthelium sabulorum* (Lam.) Gould & C.A. Clark var. *thinium* (Hitchc. & Chase) Gould & C.A. Clark], 5, FACU, Reid 9692 (Freckmann 1978)

Dichanthelium dichotomum (L.) Gould var. *nitidum* (Lam.) LeBlond, 4, Reid 9861 (LeBlond 2001)

Dichanthelium dichotomum (L.) Gould var. *roanokense* (Ashe) LeBlond, 4, Reid 9261 (LeBlond 2001)

Dichanthelium filiramum (Ashe) LeBlond, 4, Reid 9222 (LeBlond 2016)

Dichanthelium longiligulatum (Nash) Freckmann, 4, Reid 9185

Dichanthelium meridionale (Ashe) Freckmann, 4, Reid 9361

Dichanthelium neuranthum (Grisebach) LeBlond, 5, Reid 8570 (Weakley et al. 2011)

Dichanthelium oligosanthes (Schult.) Gould var. *scribnerianum* (Nash) Gould, 6, Reid 9123

Dichanthelium scoparium (Lam.) Gould, 5, FACW, Reid 9364

Dichanthelium sphaerocarpon (Elliott) Gould, 6, FACU, Reid 9543
Digitaria ciliaris (Retz.) Koel., 1, FACU, Reid 9487
Digitaria cognata (J.A. Schult.) Pilger, 6, Reid 8992
Digitaria filiformis (L.) Koel., 6, Reid 8990
Digitaria ischaemum (Schreb. ex Schweig.) Schreb. ex Muhl., 0, UPL, Reid 9589
Echinochloa walteri (Pursh) Heller, 1, OBL, Reid 9560
Eragrostis bahiensis (Schrad.) Schult., 5, FAC, Reid 8845; native according to Peterson (2003)
Eragrostis elliottii S. Watson, 5, FACW, Reid 9708
H*Eragrostis lugens* Nees, 6, FAC, Brown 8622
Eragrostis refracta (Muhl.) Scribn., 5, FACW, Reid 9691
Eragrostis silveana Swallen, 7, Reid 8719
Hordeum pusillum Nutt., 1, FACU, Reid 9127
Leersia hexandra Sw., 4, OBL, Reid 9290
Leptochloa fusca (L.) Kunth ssp. *fascicularis* (Lam.) N. Snow, 2, Reid 9559
Luziola fluitans (Michx.) Terrell & H. Rob., 1, OBL, Reid 9927
Muhlenbergia capillaris (Lam.) Trin., 7, FAC, Reid 8721
Oryza rufipogon Griffiths, 0, OBL, Reid 9918
Panicum bergii Arechav., 7, FACW, Reid 5532
Panicum brachyanthum Steud., 7, FAC, Reid 9544
Panicum dichotomiflorum Michx., 1, FACW, Reid 9512
Panicum hemitomon Schult., 5, OBL, Reid 9297
Panicum verrucosum Muhl., 5, FACW, Reid 9677
Panicum virgatum L., 7, FAC, Reid 9626
Paspalidium geminatum (Forssk.) Stapf, 3, OBL, Reid 9302
Paspalum denticulatum Trin. [Syn Paspalum lividum Trin.], 2, OBL, Brown 9724
Paspalum dilatatum Poir., 0, FAC, Reid 9594
Paspalum dissectum (L.) L., 2, OBL, Reid 9556
Paspalum distichum L., 1, OBL, Reid 9417
Paspalum floridanum Michx., 9, FACW, Reid 9715
Paspalum laeve Michx., 3, FACW, Reid 8922
Paspalum minus Fourn., 3, Reid 9381
Paspalum modestum Mez, -2, OBL, Reid 7677
Paspalum notatum Flüggé, -2, FACU, Reid 9435
Paspalum plicatulum Michx., 7, FAC, Reid 9665
Paspalum praecox Walter, 8, OBL, Reid 9540
Paspalum scrobiculatum L., 0, FACW, Reid 9426
Paspalum setaceum Michx., 6, FAC, Reid 9216
Paspalum urvillei Steud., -1, FAC, Reid 9278
Phalaris angusta Nees ex Trin., 1, FACW, Reid 9196
Phalaris caroliniana Walter, 1, FACW, Reid 9197
Poa annua L., 0, FACU, Reid 9142
Polypogon monspeliensis (L.) Desf., 1, FACW, Reid 9201
Saccharum giganteum (Walter) Pers., 3, FACW, Reid 9739

Sacciolepis indica (L.) Chase, 0, FAC, Reid 7670
Sacciolepis striata (L.) Nash, 3, OBL, Reid 9386
Schedonardus arundinaceus (Schreb.) Dumort., -1, FAC, Reid 9279
Schizachyrium scoparium (Michx.) Nash, 8, FACU, Reid 9682
Schizachyrium tenerum Nees, 10, Reid 9528
Setaria magna Griseb., 2, FACW, Doffitt 3381
Setaria parviflora (Poir.) Kerguélen, 4, FACW, Reid 9436
Sorghastrum nutans (L.) Nash, 10, FACU, Reid 9723
Sorghum halepense (L.) Pers., -2, FACU, Brown 8656
Spartina patens (Aiton) Muhl., 6, FACW, Reid 9332
Spartina spartinae (Trin.) Merr. ex Hitchc., 4, OBL, Reid 8923
Sphenopholis obtusata (Michx.) Scribn., 3, FAC, Reid 9187
H*Sporobolus compositus* (Poir.) Merr. var. *compositus*, 10, Brown 8658
Sporobolus compositus var. *drummondii* (Trin.) Kartesz & Gandhi, 10, Reid 9664
Sporobolus compositus var. *macer* (Trin.) Kartesz & Gandhi, 10, Reid 9666
Sporobolus indicus (L.) R. Br., -2, FACU, Reid 9344
H*Sporobolus junceus* (P. Beauv.) Kunth, 10, Brown 8634
Sporobolus pyramidatus (Lam.) Hitchc., 3, FAC, Reid 9623
Steinchisma hians (Elliott) Nash, 2, OBL, Reid 9170
Stenotaphrum secundatum (Walter) Kuntze, 0, FAC, Reid 9830
Tridens ambiguus (Elliott) Schult., 9, FACW, Reid 7667
Tridens strictus (Nutt.) Nash, 4, FACW, Reid 9667
Tripsacum dactyloides (L.) L., 8, FAC, Reid 9334
Vulpia octoflora (Walter) Rydb., 1, FACU, Reid 7390
Zizaniopsis miliacea (Michx.) Döll & Asch., 2, OBL, Reid 9760

POLYGALACEAE
Polygala appendiculata Vell. [syn *Polygala leptocaulis* Torr. & A. Gray], 7, FACW, Reid 9462
Polygala mariana P. Mill., 7, FACW, Urbatsch 11380

POLYGONACEAE
Polygonum caespitosum Blume var. *longisetum* (Bruijn) A.N. Steward [Syn *Persicaria caespitosa* (Blume) Nakai var. *longiseta* (Bruijn) C.F. Reed], 0, FAC, Reid 9590
Polygonum hydropiperoides Michx. [Syn *Persicaria hydropiperoides* (Michx.) Small], 3, OBL, Reid 9232
Polygonum punctatum Elliott [Syn *Persicaria punctata* (Elliott) Small], 1, OBL, Reid 9535
Rumex crispus L., 0, FAC, Reid 9150
Rumex hastatulus Baldw., 1, FACU, Reid 9804
Rumex pulcher L., 0, FACW, Reid 9189

PONTEDERIACEAE
Heteranthera limosa (Sw.) Willd., 1, OBL, Reid 9929

Heteranthera reniformis Ruiz & Pavon, 1, OBL, Reid 9914
Pontederia cordata L., 2, OBL, Reid 9451

PORTULACACEAE
Claytonia virginica L., 4, FACU, Reid 9767

POTAMOGETONACEAE
Potamogeton diversifolius Raf., 2, OBL, Reid 9913

PRIMULACEAE
Anagallis arvensis L., 0, FACU, Reid 9156
Anagallis minima (L.) Krause, 1, FACW, Reid 9113
Samolus ebracteatus Kunth, 7, OBL, Reid 8374

RANUNCULACEAE
Clematis crispa L., 3, FACW, Reid 8917
Ranunculus laxicaulis (Torr. & A. Gray) Darby, 3, OBL, Reid 9139
Ranunculus pusillus Poir., 1, FACW, Reid 9132
Ranunculus sardous Crantz, 0, FAC, Reid 9193

RHAMNACEAE
Berchemia scandens (Hill) K. Koch, 1, FAC, Reid 9367

ROSACEAE
Prunus serotina Ehrh., 1, FACU, Reid 9366
Rosa bracteata J.C. Wendl., -2, UPL, Reid 9759
Rubus argutus Link, 1, FAC, Reid 9757
Rubus trivialis Michx., 2, FACU, Reid 9536

RUBIACEAE
Diodia teres Walter, 3, FACU, Reid 9545
Diodia virginiana L., 3, FACW, Reid 9342
Galium tinctorium (L.) Scop., 2, FACW, Reid 9200
Houstonia pusilla Schoepf, 1, FACU, Reid 9765
Houstonia rosea (Raf.) Terrell, 4, Reid 9766
Oldenlandia boscii (DC.) Terrell, 2, FACW, Reid 9744
Oldenlandia uniflora L., 2, FACW, Reid 9523
H*Stenaria nigricans* (Lam.) Terrell, 8, Correll 9582

RUTACEAE
Zanthoxylum clava-herculis L., 2, FAC, Reid 9750

SALICACEAE
Salix nigra Marshall, 1, OBL, Reid 9925

SAPOTACEAE
Sideroxylon lanuginosum Michx., 3, FACU, Reid 9756

SAXIFRAGACEAE
Lepuropetalon spathulatum Elliott, 2, FACW, Reid 9763

SCROPHULARIACEAE
Agalinis fasciculata (Ell.) Raf., 4, FAC, Urbatsch 11366
Agalinis oligophylla Pennell, 5, FAC, Reid 7271
Agalinis viridis (Small) Pennell, 5, Reid 8363
Bacopa caroliniana (Walter) B.S.P., 4, OBL, Reid 9446
Bacopa monnieri (L.) Pennell, 2, OBL, Reid 9853
Bacopa rotundifolia (Michx.) Wettst., 2, OBL, Reid 9555
Buchnera americana L., 8, FAC, Reid 9223
Gratiola brevifolia Raf., 7, FACW, Reid 9163
Gratiola pilosa Michx., 6, Reid 9531
Gratiola virginiana L., 2, OBL, Reid 9111
Lindernia dubia (L.) Pennell var. *anagallidea* (Michx.) Cooperr., 1, OBL, Reid 9557
Mecardonia acuminata (Walter) Small, 4, FACW, Reid 9618
Micranthemum umbrosum (J.F. Gmel) S.F. Blake, 2, OBL, Reid 9300
Nuttallanthus canadensis (L.) D.A., 1, Reid 9218
Penstemon laxiflorus Pennell, 8, FAC, Reid 9226

SMILACACEAE
Smilax bona-nox L., 1, FAC, Reid 9730
Smilax rotundifolia L., 1, FAC, Reid 9527
Smilax smallii Morong, 1, FACU, Reid 9460

SOLANACEAE
Physalis pubescens L., 2, UPL, Reid 9458
Physalis pumila Nutt., 7, Reid 9134
Solanum carolinense L., 1, FACU, Reid 9137
Solanum ptycanthum Dunal, 1, FACU, Reid 9349

SPHENOCLEACEAE
Sphenoclea zeylanica Gaertn., 0, FACW, Reid 9519

STERCULIACEAE
Melochia corchorifolia L., 0, FAC, Reid 9909

ULMACEAE
Celtis laevigata Willd., 1, FACW, Reid 9924
Ulmus alata Michx., 1, FACU, Reid 9608

VERBENACEAE
Callicarpa americana L., 2, FACU, Reid 9368
Phyla nodiflora (L.) Greene, 2, FAC, Reid 9356
Verbena brasiliensis Vell., -1, Reid 9576
Verbena halei Small, 2, Allain 1569 (USGS)

VIOLACEAE
Viola lanceolata L., 8, OBL, Doffitt 3371

VITACEAE
Nekemias arborea (L.) J. Wen & Boggan [Syn *Ampelopsis arborea* (L.) Koehne], 2, FAC, Reid 9731

XYRIDACEAE
Xyris ambigua Bey. ex Kunth, 8, OBL, Reid 9908
Xyris difformis Chapm. var. *difformis*, 6, OBL, Reid 8366
Xyris laxifolia Mart. var. *iridifolia* (Chapm.) Kral, 6, OBL, Reid 9930

VITA

Christopher Simon Reid is a native of St. Francisville, Louisiana. He holds a bachelor's degree in forestry from Louisiana State University (LSU) and a master of science from The University of Louisiana at Monroe. He entered the graduate program in Biological Sciences in 2009 and will receive his doctoral degree in December of 2016. Following graduation, he will continue to work as a botanist with the Louisiana Department of Wildlife and Fisheries, where his primary focus is coastal prairie habitat restoration. He will continue to teach field botany courses at LSU.